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HYBRIDIZATION IN NATURE BETWEEN SPECIES OF CATOSTOMID FISHES

BY

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INTRODUCTION

It may now be regarded as well established that distinct species and even genera of fish hybridize in nature, at times with considerable frequency. The natural crossing of species has a bearing on several lines of biological inquiry—growth, nomenclature, speciation, genetics, and wildlife management—and consequently calls for a thorough analysis. To ensure an intensive and compact treatment we have selected for the present study the hybrids which we have thus far recognized in the Catostomidae, a single family of almost exclusively North American fresh-water fish. Much work has been published[1] in both Eurasia and America on interspecific combinations in the closely related family Cyprinidae, but no hybrids between catostomid fishes (the "suckers") have previously been described.

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[1] Some key references on interspecific cyprinid hybrids are: Heincke (1892), Hubbs and Brown (1929), Schmidt (1930), Hubbs and Schultz (1931), Matsui (1931), Berg

This paper is the product of a division of labor. Carl L. Hubbs made the identifications of the hybrids and is responsible for most of the interpretive treatment. Laura C. Hubbs carried out the almost endless mathematical calculations. Raymond E. Johnson, as research assistant, made nearly all of the counts and measurements (about 2000 on the hybrids and a much larger number on the parental species). We joined in planning and carrying on the details of the investigation and in preparing the report.

Grants from the Horace H. Rackham School of Graduate Studies, of the University of Michigan, made it possible to conduct this analysis and to publish the results. The gifted hand of Grace Eager produced the pictures of the lip structures, which illustrate well the intermediate characters of the sucker hybrids. Leonard P. Schultz collected many of the specimens studied, and collaborated in the first identification of hybrids between *Catostomus macrocheilus* and *C. syncheilus;* he has also loaned us 2 specimens from the National Museum collections. Robert R. Miller carried out the field work on the hybridization between *Catostomus,* species, and *Pantosteus santa-anae* and collected part of the *Catostomus tahoensis* × *Pantosteus lahontan* material. Professor Cecil C. Craig, of the Department of Mathematics in the University of Michigan, derived for us a formula for determining the standard error of the hybrid index (as described below).

MATERIALS AND METHODS

The natural hybrids analyzed in this paper were obtained in the course of the systematic study of North American fresh-water fishes which has been stressed at the University of Michigan Museum of Zoology since 1920. Of the 182 hybrid suckers studied, 76 represent 3 hybrid crosses in the genus *Catostomus* and 105 exemplify 7 hybrid combinations between species of the genera *Catostomus* and *Pantosteus*.

Only a few of the specimens were recognized as hybrids in the field, and even then the collections may be regarded as random, in regard to the numbers of hybrids and of parental species. When the hybrids were identified in the field, as in Sucker Creek, Oregon (where *Catostomus macrocheilus* and *Catostomus syncheilus syncheilus* cross), further collecting was designed to secure series as large as possible, not only of the heterozygotes but also of the parental types. The only trip made for the special purpose of securing additional specimens of hybrid suckers in streams where they are known to occur was to Sespe Creek, California, where *Catostomus,* species, and *Pantosteus santa-anae* cross. Additional material of any available suckers, to augment the hybrid material, was otherwise specifically sought only once—

(1932–33), Schultz and Schaefer (1936), Geyer (1937), Raney (1940*a* and *b*), and Hubbs and Miller (1943). A large number of other references are given in Dean's *Bibliography of Fishes* (1923, 3: 505–7) and in the *Zoological Record.*

from the Colorado River drainage basin of Colorado, where the apparently introduced *Catostomus commersonnii sucklii* was found to be hybridizing with a native sucker, *Pantosteus delphinus delphinus.*

All of the material reported on in this paper is contained in the Museum of Zoology of the University of Michigan (U.M.M.Z.).

The methods of study were those employed in the more precise systematic investigations of the present day. The suspected hybrids were scrutinized for any possible characters of structure, form, or color, by which they might show their relationship to the presumed parental species. Special attention was paid to diagnostic features in the structure of the mouth (Pls. I, II, and VI): the degree to which the upper lip is flattened out; the tendency for the outer face of the upper lip to be smoother (less papillose) than the inner face, and to be ridged and reflected so as to partly cover the inner surface; the presence or absence of an emargination at the outer lateral angles of the mouth; the depth of the median incision between the lobes of the lower lip, the width of the union in front of the incision, and the number of rows of papillae crossing this isthmus; the width, strength, and shape of the cartilaginous ridges of the jaws, inside the upper and the lower lip; the degree to which the gape is arched, or transverse; and the width and the length of the mouth. The size, shape, and prominence of the snout were also emphasized.

In order to permit statistical analysis of differences in proportions and of differences in the numbers of dorsal fin rays and of scales, all measurements and counts thought to be critical and obtainable with accuracy were made. These determinations were taken according to the methods outlined by Hubbs and Lagler (1941: 12–20). The predorsal length, as here given, is the distance from the tip of the snout to the front of the small, embedded predorsal plate, at a place where, upon slight pressure, the divider point comes to rest. The width of the mouth is the greatest over-all measurement, taken after the lips, if distorted in preservation, have been molded into approximately normal shape. The length of the union of the lower lip is the distance along the mid-line from the front of the cartilaginous ridge of the lower jaw to the point of the V along the extreme posterior edge of the lip, disregarding the shallow groove which extends some distance forward.

Measurements of the appropriate parts of the body were taken with a dial caliper reading to 0.1 mm. and estimated to 0.01 mm. Such refinement has little significance with the larger dimensions, but is important as a source of avoiding errors in measuring small parts. The measurements are calculated as thousandths of the standard length.

Comparable counts and measurements were made on selected material of the parental species as well as on the hybrids. An effort was made to find specimens of the species which were from the same locality as the hybrids and which were about the same size. When such material was not available, examples which were as nearly the same size as could be found were selected from as near by as possible. When they covered a considerable size range the hybrids and parental species were divided into size groups of limited extent, so as to render the proportionate measurements reasonably comparable. These groupings are indicated in the table of proportions for each hybrid combination. The method of relative-growth analysis is more precise, but was not thought practicable for this study because of the small number of hybrids.

The method of counting the pelvic rays needs some comment, as the number of rays in this fin provided a valuable check on the interpretation of 2 types as hybrids. Pelvic ray counts are not generally listed in systematic descriptions of suckers though they have been shown to be of value in this family (Hubbs, 1930: 20–21, 37). The sum of the counts of both fins is the unit of tabulation. A variable sliver-like ray at the outer edge of the base of the first main ray is disregarded. Each of the 2 to several rays that are often approximated or even partly fused is included in the count. Occasional fins that are lacking, rudimentary, defective, or obviously injured are not counted.

In the tabulations and computations all counts for each stated combination were treated as a single statistical array for all the hybrids and for all the specimens studied of each parental species. In contrast, the computations based on measurements were made separately for each size group at each locality.

The means and their standard errors are given. The standard errors of the means (S.E.) were computed according to the formula

$$(1)\quad \text{S.E.} = \frac{\sigma_V}{\sqrt{N}}$$

The standard deviation (σ_V) of the noncontinuous variates was obtained according to the commonly used formula

$$(2)\quad \sigma_V = \sqrt{\frac{\Sigma d^2}{N-1}}$$

The coefficient of variability is

$$(3)\quad V = \frac{100\,\sigma_V}{M}$$

The counts are all tabulated according to the hybrid combinations (Tables XXXII to XXXVII). Because of the variations with age and locality, no simple frequency tabulation of the proportionate measurements is warranted. We can, however, obtain figures (hybrid indices) which portray the relation of each measurement in each hybrid to the mean value for each parental species of a comparable size group from the same or an approximate locality. We can then combine these indices in any way that is desirable.

Character Index

Owing to the approximation of their characters and to the considerable individual variability which they display in each respect, it is difficult to identify suckers and their hybrids on the basis of single traits. The use of combinations of characters leads to more certain identifications. For this reason we have found character indices of particular value in the present study.

The term "character index" was proposed by Hubbs and Whitlock (1929: 470), who found the need for a simple mathematical expression of several differential features. Following this introduction, character indices have been successfully applied in fish systematics for the separation of closely allied forms by Koelz (1929: 426), Schultz and Welander (1934: 6), Hubbs and Cannon (1935: 27), Schultz and Thompson (1936: 74–75), Hubbs (1936: 189–93 and 249–50), Hubbs and Kuhne (1937: 13–14), Schultz (1937: 19–20), Schultz and Reid (1937: 211–12), and in a few other works. Schultz and Schaefer (1936: 5–8) first applied a character index in the determination of fish hybrids. Hartweg (1938: 3–5) and Woodbury and Woodbury (1942: 138), respectively, applied the method in chelonian and ophidian systematics.

The character index, under the name of "general index" or "aggregate difference," has also been introduced in botany (Anderson and Whitaker, 1934: 35–38, Fig. 4; Anderson and Abbe, 1934: 43–49, Fig. 1; Stebbing, 1942: 228–30). The method of computation of the botanist's index (taking the square root of the sums of the squares of the individual differences) has not been employed in ichthyology, but the scope and significance of their index, as stated, is the same as that of the ichthyologist's character index. It is of some interest that methods for summarizing characters into a single index figure were independently proposed by botanists and ichthyologists.

The use of character indices and of other statistical combinations of characters, such as the physical anthropologist's "coefficient of racial likeness," has lately been severely criticized by Ginsburg (1939). We see no reason, however, to doubt the value of the method. Proportions and ratios, long used in systematic ichthyology, are simple character indices—these, no one queries. It is the somewhat more complicated formulae that, on first attention, may appear to be incongruous or to be the mere juggling of figures. No arithmetic combination of characters, however, can bring out differences which do not exist, so long as we apply the identical character-index formula to both types being compared. When the data are limited a source of error may lie in the selection of character combinations that happen to yield results in line with expectancy.

Contrary to Ginsburg's claim, character indices may measure not only the significance of differences but also degrees of divergence. Very few, if any, kinds of animals differ in a single character. The forms are separated by combinations of characters. Races and subspecies, as well as "good species," tend to exhibit what Goldschmidt (1940) has called "different reaction systems" (Hubbs, 1941*c*: 276). Since the types are inherently characterized by combinations of characters, the validity and the amount of their differentiation might often be better indicated by indices which measure several features than by simple counts or measurements of single traits. Only the real difference between 2 populations is shown by a character index which, on the basis of adequate samples, largely or wholly eliminates the overlap in frequency distribution that is evident when one considers separately the traits which were combined to form the index. Forms which differ consistently in an ensemble of characters must have attained full specific distinction.

The computation of a character index somewhat resembles the action of the mind in the impressionistic identification of kinds of organisms. The experienced mind which with little error can distinguish Japanese from Chinese men synthesizes a large number of more or less unrelated features, any one of which if measured and analyzed would show a great overlap in frequency distribution.

One main advantage of a character index—and this advantage tends to accrue, the larger the number of traits combined—lies in the fact that a character aberrant enough to cause one form to resemble another with which it is being compared tends to be offset by other characters which will probably not vary in the same direction. The character index gives joint expression to a number of traits, minimizing the importance of extreme fluctuations in single features.

The present work provides examples of the utility of a character index in sharpening the expression of the difference between populations; in our case between a hybrid and each of its parental species. Thus, a character index (Table V; Fig. 1) based on the scale and ray counts of *Catostomus macrocheilus*, hybrids, and *C. syncheilus* shows the relations between the hybrid and its parent species much more emphatically than does any of the sets of counts considered alone (Tables XXXII–XXXVII; Fig. 7). Again, subtracting certain scale counts that are low in one type from those that are high in the same form, gives us an especially sharp and valuable indication (Table XVIII; Fig. 5) of the difference between certain hybrids and their parental species. The difference thus shown is a true one, reflecting only what exists in the organisms—in no sense an artificial concoction.

Some doubts may arise as to the statistical treatment of character indices, but we have been informed by statisticians that such values as standard deviation, standard error, and the like may legitimately be computed for an array of the indices, provided that each of the combined characters presents in itself an approximately normal frequency distribution. This proviso will ordinarily be met.

Hybrid Index

The hybrid index, a special type of character index, is designed as a simple expression of the relationship of the traits of the hybrid to those of the parental species. It may be obtained separately for each character of each hybrid specimen, and the individual indices may then be tabulated for all the hybrids to show, for example, how the average number of dorsal rays or the average width of the mouth of the hybrids, as a group, compares with the mean value for each parental form (Table XXXVIII). Also, the separate indices for all traits in any given hybrid specimen may be averaged so as to indicate how the individual, in the ensemble of its characters, compares with each parental type (Table XXXIX; Fig. 8).

Anderson (1936) proposed such an index for the analysis of plant hybrids, and his method has been followed by other plant geneticists and systematists (cited by Riley, 1939). This method is not regarded as adequate for the analysis of fish hybrids. It assigns the value 0 to the measurement or count of one species, 2 to that of the other parental form, and 1 to that of the hybrids, if they are intermediate. But there are all degrees of intermediacy, and every gradation from the one parental type to the other.

A somewhat similar method for computing a hybrid index has just been used by Ripley (1942: 57–58, Fig. 1), in an analysis of hybridization between species of birds. By judging the differential degree of resemblance Ripley assigned scores for each character, on a scale grading from 0 for one parental species to 10 for the other, and then averaged these scores for each hybrid specimen, so as to provide a numerical expression of its similarity to each species.

The hybrid index as here used was introduced by Hubbs and Kuronuma (1942: 291). In any comparison each individual or average index is expressed as a figure on a scale of 100, in which the average value for the one parental type is set at 0, and that for the other parental type at 100. With V_H representing the value of the character of the hybrid, M_1 the mean value for parent, 1, and M_2 the mean for parent 2, the formula is, therefore:

$$(4)\quad \text{Position of the hybrid (P)} = \frac{V_H - M_1}{M_2 - M_1}$$

$$(5)\quad \text{Hybrid index (I)} = 100\ \text{P}$$

In the present paper we have applied M_1 to the parental species which seems to be the more primitive. This is the coarse-scaled, short-nosed species in the *Catostomus* × *Catostomus* crosses, and the *Catostomus* species in the *Catostomus* × *Pantosteus* hybrids. It is recommended that such practice be followed whenever a decision as to differential primitiveness is feasible.

It will be noted that a hybrid index of 50 denotes exact intermediacy between the parental types. A summary index of 25 in a *Catostomus* × *Pantosteus* hybrid would indicate a correspondence 3 times closer to the *Catostomus* parent than to the *Pantosteus*.

The hybrid index is of particular service in testing the assumption of hybridity and the mode of inheritance. If the assumed hybrids are merely selected specimens of the 2 species, or if characters show strict Mendelian segregation, the individual indices when combined would show a bimodal frequency distribution with modes close to 0 and to 100 on the scale mentioned above. A unimodal curve with the peak near 50 would confirm the interpretation of the aberrant specimens as hybrids, and would indicate a multiple-factor type of inheritance for systematic characters (or—as a generally improbable contingency—merely a lack of dominance). Should the values for 2 or more unrelated traits in a given set of hybrids yield such unimodal curves, intervening between those for the parental species, the assumption of hybridity would appear to be well established.

An average index of about 50 could be obtained by mixing typical specimens of each form, or through Mendelian segregation, which would cause the hybrids to resemble one parental species in some respects and the other parental type in other characters. But in either case the frequency distribution would be bimodal. The fact that the summary indices for all characters for each individual tend to average near 50 might also result from a mixture of specimens of the 2 types or from genetic segregation. To clarify the situation, therefore, the indices need be summarized for single characters and for all characters, as well as for individual fish.

The hybrid index is computed directly for hybrid populations by substituting the mean value of the hybrids (M_H) for V_H in formula (4).

When the number of hybrids and of each parental species approximates or exceeds 30, when the frequency distribution is approximately normal (as it usually is), and when the dispersion of the difference between the values for the 2 species is relatively small as compared with the difference between the average for the parental forms, it is possible to make an approximate computation of the standard error of the hybrid index ($S.E._I$) as follows:

$$(6)\quad S.E._{I} = 100\sqrt{\frac{\dfrac{\sigma_1^2+\sigma_2^2}{(M_2-M_1)^2}\left[P^2-2P\dfrac{\sigma_1^2}{\sigma_1^2+\sigma_2^2}+\dfrac{\sigma_H^2+\sigma_1^2}{\sigma_1^2+\sigma_2^2}\right]}{N_H}}$$

In this formula $\sigma =$ standard deviation of the mean (M); the subscripts refer to parent 1, parent 2, and the hybrid; P is the position of the hybrid (formula 4); and N_H is the number of hybrids.

CRITIQUE ON SUPPOSED HYBRIDIZATION BETWEEN SPECIES OF *MEGASTOMATOBUS, ICTIOBUS, CARPIODES,* AND *MOXOSTOMA*

Before presenting our original data we consider the only previously published statement on hybridization in the Catostomidae. Thompson (1935: 492–93) wrote:

> While it has not been proved that the so-called "mongrel" buffalo, *Ictiobus urus,* is really a hybrid between the other two native species, there is a considerable body of circumstantial evidence to indicate that such is the case. Some of the difficulties of identification in the genus *Carpiodes* and in the genus *Moxostoma* may be attributed to occasional hybridization within these genera.

Issue may be taken with these statements. Difficulty of identification in the genera *Ictiobus, Carpiodes,* and *Moxostoma* is admitted, but appears to be due not to hybridization but rather to 2 other factors: (1) a tendency for the species to be characterized by a combination of traits, none of which by itself may be invariably distinctive; (2) a common failure to recognize or to appreciate all of these characters. The rather clear diagnoses of the species of *Ictiobus* (including *Megastomatobus*) and of *Carpiodes,* given by Forbes and Richardson (1909, and 1920: 68–80) were supplemented by the study of Hubbs (1930: 8–16). Most of the characters of the Mississippi and Great Lakes species of *Moxostoma* are rather weakly distinctive when considered individually, but are adequate for identification when taken in combination (Hubbs, 1930: 16–32). When all the characters presented by these authors are taken into account and the specimens are subjected to intensive study, doubt seldom need arise concerning the specific identity of any of the suckers of the Mississippi Valley and Great Lakes region (with the probable exception of 3 pairs of species, discussed below).

The suggestion that *Ictiobus urus* (=*I. niger*) may represent hybrids between *Ictiobus* (=*Megastomatobus*) *cyprinella* and *Ictiobus bubalus* finds very little if any confirmation. It is true that some of the characters of *I. niger* are intermediate between those of *M. cyprinella* and those of *I. bubalus,* but other features of *I. niger* are not intermediate. Apparently having in mind the idea of hybrid origin expressed in the fisherman's vernacular name, Forbes and Richardson held:

> The mongrel buffalo [*I. niger*] appears to vary somewhat more than either *I. cyprinella* or *bubalus,* but we have met with no cases which appear to show intergradation with either. This species seems to be always distinguishable from the former by its much smaller and less oblique mouth, the upper lip falling far below the level of the lower margin of the orbit, and by the coarsely striate lower lips; from the latter by the more elongate and less compressed body, and by the broad rounding of the frontal region and of the back in front of the dorsal fin.

In the anatomical characters treated as of generic implication (Hubbs, 1930: 8), *Ictiobus niger* agrees with *I. bubalus,* and both these species therefore contrast sharply with *Megastomatobus* (the only partial exception to this statement involves mouth structures). Krumholz (1943: 37–38, Pl. 1) finds not only that *I. niger* is sharply distinctive in the characters of the Weberian ossicles, particularly in the sculpturing of the tripus, but also that it is not intermediate in these features. *Ictiobus niger,* therefore, does not conform to the virtually universal rule (Hubbs, 1940: 205–9) that interspecific hybrids have uniformly intermediate characters. In general, *I. niger* is associated with the 2 other species, but it occurs alone in parts of its range (Hubbs, 1930: 11; Hubbs and Lagler, 1941: 41), therefore, in places where hybridization would not be expected.

The theory of hybridization between *Megastomatobus cyprinella* and *Ictiobus bubalus,* at least as a common phenomenon, seems ruled out by the evidence. It would be difficult to prove, however, that hybridization does not take place between some of the more closely related species in the Ictiobinae. Because of extensive variation in each species of the 3 following combinations, it would be hazardous to identify hybrids between: *Ictiobus* *niger* and *I. bubalus; Carpiodes forbesi* and *C. cyprinus; Carpiodes carpio* and *C. velifer.*

These pairs are trenchantly distinguished from other pairs, but the 2 members of each unit have very similar characters (Hubbs, 1930: 8–18). The distinctive features—parallel within each of the 3 pairs—mainly involve depth and compression of body, the expanse of the fins (particularly the dorsal), and the size of the eye. The first-named member of each pair is a slenderer, thicker fish than its cognate and has a lower dorsal fin, a larger mouth, and a smaller eye. These characters, however, exhibit so much individual and age variation that it is extremely hard at times to separate the related forms. It seems probable that the difficulties encountered in separating *I. niger* from *I. bubalus,* or *C. forbesi* from *C. cyprinus,* or *C. carpio* from *C. velifer* are due to an inadequate comprehension of these variations, to the closeness of the characteristics, or to insufficient analytical study. It cannot be regarded as demonstrated, however, that hybridization or intergradation does not occur between the 2 cognate species in each of the 3 pairs.

Until the material was re-examined in the preparation of this paper, we thought that we had sufficient evidence to indicate the occasional hybridization in nature between species of *Moxostoma.* Mention may be made of the 2 specimens formerly treated as hybrids in this genus, because they serve as examples of pitfalls into which one may stumble unless the identification of natural hybrids be made in a critical spirit and with full knowledge of the facts involved.

One of the 2 specimens, an adult from the Muskegon River, Michigan, showed, when fresh, colors intermediate between those of *Moxostoma rubreques* and *M. erythrurum* (with which it was collected). Some of the counts and measurements intervened between those of the supposed parental species; other characters were similar to those of each species. A hybrid index of 47 indicated only a 3 per cent divergence from exact intermediacy. Confirmation of the hybrid interpretation seemed to come from a special measure of the degree of falcation or roundness of the dorsal fin, obtained by dividing the length of the eighth dorsal ray into that of the first principal ray, with results as follows:

In 9 comparable specimens of *M. rubreques*	1.27 to 1.37	(average, 1.32)
In the 1 specimen misidentified as a hybrid	1.47	
In 8 comparable specimens of *M. erythrurum*	1.40 to 1.67	(average, 1.58)

On final recheck, however, it was thought possible that this specimen might be an example of *Placopharynx carinatus,* from beyond its supposed limits of distribution. An examination of the molar pharyngeal teeth verified this suspicion. It was just a coincidence that in certain respects this specimen of *Placopharynx* proved intermediate between 2 species of *Moxostoma.*

Another specimen of *Moxostoma,* taken with *M. aureolum* and *M. anisurum* in the Mississippi River, Wisconsin, was long interpreted as a hybrid between those species. The feature that first attracted attention was the intermediate form of the lips (Pl. II, Figs. 3*a–c*). The fish was deeper and heavier-set than the usual (though not the extreme) *aureolum*, even deeper than the average *anisurum*. In some measurements it proved intermediate, in others beyond the range connecting the averages for the 2 species. The hybrid index was computed as 46, strongly verifying the assumption of hybrid origin. Yet other characters, such as the number of dorsal rays (12), the length of the dorsal base (about two-thirds distance forward to occiput), the length of the depressed dorsal (about equal to the dorsal–occiput interspace), the sharp point and moderate falcation of the dorsal fin, and the dark bases of the scales, were wholly typical of *aureolum*, not approaching the expression of these characters in *anisurum* (Hubbs, 1930: 16–32). Such is not the genetic behavior of hybrids between systematic forms. Judgment was accordingly revised; the specimen was reidentified as an aberrant example of *M. aureolum* in which, for some reason, the juvenile V-shaped form of the lower lip was retained in the half-grown (the size at which the lip becomes truncate varies greatly).

We are therefore able to present evidence for interspecific catostomid hybrids only within the genus *Catostomus* and between that genus and *Pantosteus.*

IDENTIFICATION OF NATURAL HYBRIDS BETWEEN SPECIES OF CATOSTOMIDAE

A skeptical attitude should obviously be maintained toward the identification as interspecific hybrids of any fish specimens collected in nature. Since ordinarily the evidence for such an interpretation will remain circumstantial, every effort should be made to exclude other plausible explanations. Needless to say, the trustworthy identification of natural hybrids calls for a thorough knowledge of the systematics of the group.

We have striven to avoid errors of interpretation in the identification of the catostomid hybrids. The supposed hybrid specimens have been thoroughly examined, and many diagnostic counts and measurements taken for detailed comparisons. Their characters have been compared with those of all species which were taken at the same place, or which might be expected to occur there. Due consideration has been given the possibility that the aberrant features of the presumed hybrids were caused by modification or mutation, for it is well known that the characters of one species may be altered to approach or even to correspond with those of a related species (witness the recent study on *Catostomus* by Hubbs, 1941*a*). The heredity that would have been involved in the production of the sucker specimens interpreted as hybrids has been compared constantly with the known genetics of experimentally induced hybrids in other families of fishes.

Circumstantial evidence of a varied nature has led us to diagnose certain suckers as hybrids. It was first determined that an apparent hybrid had characters that exclude it from the limits of normal variation of any species which does or may occur in the same region, or which might have wandered or have been transplanted therein. It was seen not to have the earmarks of a mutant sport. It was determined that all the appreciable characters of the "hybrid" were plausibly to be interpreted as the genetic result of the crossing of 2 species which are known to live in the same water or which can reasonably be assumed to occur there. It was thought legitimate to expect that hybrid suckers would follow the general rule (Hubbs, 1940: 205–9) that interspecific hybrids tend to be intermediate between the parental species in all systematic characters.

Careful consideration was given to the possibility that the presumed hybrids might represent hitherto undescribed species. The argument against such an interpretation usually ran as follows: the aberrant fish are too few to represent an established species, in regions as well worked as those from which the hybrids came, and they are too uniformly intermediate between the presumed parental species, both of which occur in the same area. In various features of distribution and ecology as well as in characters, they are most plausibly to be interpreted as hybrids and correspond with authenticated species-crosses in other groups.

The intermediate characters serve most strikingly as evidence for hybridity, when the supposed parental species are separated generically. Throughout many of the waters of western North America the suckers are referable to 2 types, known as *Catostomus* and *Pantosteus*. Ordinarily, these types remain sharply distinct, particularly in the structure of the mouth (Pl. I). Only occasional specimens (those interpreted as hybrids) are sufficiently intermediate in mouth characters to break down the distinction.

The same specimens that show intervening features in one set of characters, such as mouth structure, are also intermediate in various other features of form, counts, and measurements. Nowhere have breeding populations of the intermediate types been collected. They do not have the attributes of species. The only interpretation that fits the facts is that these aberrant specimens are the product of the natural crossing of distinct species.

Most of the hybrids were accorded the final identification on first examination, so striking was the intermediacy in appearance. A shift in opinion on further analytical study was made only for 2 specimens of the *Moxostoma* group (described above) and for a few young of the *Catostomus macrocheilus* × *Catostomus syncheilus* series.

Perhaps the most serious initial doubt was involved in the identification of certain suckers from the Colorado River system of Colorado as hybrids between *Catostomus commersonnii sucklii* and *Pantosteus d. delphinus*. In the first set obtained, the hybrids were small; and no coarse-scaled *Catostomus* of any kind was known from the upper waters of the Colorado system. The occurrence there of such a species was called for, however, to explain the source of the characters of the hybrids, of which *Pantosteus delphinus* (taken there) was obviously one parental species. The second parent was identified as *Catostomus commersonnii sucklii* on the seemingly hazardous assumption that this species of the Mississippi Valley had been transplanted (as bait?) across the Continental Divide. A suggestion that this might have happened came from the inclusion of 2 Mississippian minnow species (*Semotilus a. atromaculatus* and *Pimephales p. promelas*) in the small series containing the unexpected hybrid. This collection was seined in the headwaters of the Colorado River at Hot Sulphur Springs, Colorado. We have been informed that this is a favorite fishing spot for residents of Denver, who may very well have carried live bait minnows across the divide; and in 1942 we noticed that this stretch of water was being heavily fished by Colorado residents (mostly fly-fishermen, however). After the Hot Sulphur Springs collection was studied, material of *Catostomus commersonnii sucklii,* as well as of *Pantosteus d. delphinus* and of 2 additional hybrids between these species, was taken in the Colorado River system of southwestern Colorado. The original diagnosis was thus upheld. Furthermore, the first *Catostomus catostomus griseus* to be recorded from the Colorado River drainage was included, to confirm the view that fishes native to the eastern drainage have somehow gotten over the Continental Divide. The accidental transfer of another bait fish across the Continental Divide has recently been reported by Simon (1942: 7, 17), who wrote that *Platygobio gracilis* has thus become established in the Snake River system. That *Catostomus commersonnii sucklii* and *Catostomus catostomus griseus* (and *Semotilus* and *Pimephales*) are not native in the Colorado River system is indicated by the reports of Jordan (1891), Ellis (1914), and all other ichthyologists who have worked in the Rocky Mountain region.

Mr. C. N. Feast and John D. Hart of the Colorado Fish and Game Commission have just told us that they too think that Platte River suckers have been introduced into the Colorado River system. Suckers first appeared in the South Mesa Lake country in the Colorado headwaters about 1926, and it is thought that they were carried over by bait fishermen, perhaps by Japanese farm laborers, who were brought in about that time. Since then, suckers, thought not to be of the native species, have multiplied so fast in the Colorado River waters as to become a problem.

With the exception of the above-mentioned collection from Hot Sulphur Springs, both presumed parental species were taken with the hybrids, or, in the case of small collections, at a locality near by. When all the available evidence is considered, it seems obvious that both parental kinds live wherever hybrid suckers occur.

One of the strongest lines of evidence in favor of our interpretation of certain suckers as hybrids is the circumstance that these specimens are intermediate between the specific parental types occurring in the same region. Thus, the specimens regarded as hybrids between *Catostomus* and *Pantosteus* are not only intermediate between the 2 genera but also show their affinity to the particular species of these genera with which they were taken. The evidence for this statement can be adduced from the detailed accounts for each combination and is well shown in the comparative drawings of lip structure (Pl. I).

Unfortunately, no opportunity has arisen in the present study to confirm by breeding experiments or by cytological observations the strong circumstantial evidence that the supposed hybrid suckers are really the result of interspecific crossing. However, all the available systematic and natural history information checks with the data on hybrid combinations which have been verified by controlled matings; by observations of the 2 supposed parental species spawning together in nature; by evidence of hybrid vigor in growth, pigmentation, etc.; and by peculiarities in the cytological structure and in the behavior of the gametes. Such confirmation has been provided in some of our other studies (as those of Hubbs and Hubbs, 1932–33).

HYBRIDS BETWEEN SPECIES OF *CATOSTOMUS*

Except for the combination of *Catostomus macrocheilus* with 2 subspecies of *Catostomus syncheilus,* hybrids within the genus *Catostomus* prove to be extremely rare. This rarity of hybrids is due in part only to the circumstance that a single species of *Catostomus* occurs over much of the range of the genus; there are large areas in which 2 species live together. The 5 known *Catostomus* × *Catostomus* specimens, other than those between the 2 Columbia River basin species named above, are referable to the cross:

1. *Catostomus commersonnii sucklii* × *Catostomus catostomus griseus*

(Pl. II, Fig. 2*b*; Pl. III, Fig. 2)

U.M.M.Z.[1] No. 105634: 1 yearling 68 mm. in standard length, collected by W. Petravicz and Middendorf in the North Fork of South Platte River near Pine, Jefferson County, Colorado, at an altitude of 6900 feet; July 20, 1938.

U.M.M.Z. No. 132230: 1 half-grown 151 mm. long, seined by Carl L. Hubbs and family in Laramie River (tributary of North Platte River), east of Bosler, Albany County, Wyoming, at an altitude of about 7000 feet; September 17, 1934.

U.M.M.Z. No. 135190: 2 young and 1 yearling, 33, 44, and 101 mm. long, taken by Raymond E. Johnson and Paul Romberg in North Platte River near Henry, Scotts Bluff County, Nebraska; July 23, 1940.

No specimens of *Catostomus commersonnii sucklii* were included in the small collection containing hybrid specimen, U.M.M.Z. No. 105634, but examples of this parental species were secured by the same collectors near by. No other species of *Catostomus* occur in the region. After re-examining their material we can affirm that Evermann and Cox (1896: 391) erred in referring the fine-scaled suckers of the Platte River system to 2 full species, *C. griseus* and *C. catostomus.* Our studies have led to the conclusion that *griseus* is the southern, montane representative of *C. catostomus* and that it differs from the typical subspecies most noticeably in the greater height and width of the snout, which is less pointed in either dorsal or lateral aspect: except in fish less than 100 mm. long the least distance between the nostrils is more instead of less than two-thirds the postorbital length of the head (Table III).

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[1] U.M.M.Z. refers to the catalogue of fishes in the University of Michigan Museum of Zoology.

There are some indications that *C. c. griseus* may include 2 recognizable races, a fine-scaled mountain form and a relatively coarse-scaled one on the Plains. Unless this be true one might conclude that there is, or has been, considerable hybridization on the Plains between *griseus* and the very coarse-scaled Plains white sucker, *C. commersonnii sucklii* (see Evermann and Cox, 1896: 392–94). In other characters, however, the Plains specimens of *griseus* with as few as 83 to 90 scales in the lateral line (including those so identified by Evermann and Cox) show no distinctive approach toward *sucklii;* we regard them as direct variants of *griseus,* rather than as products of recent or past hybridization. Southern, lowland, and other warm-water races in fishes commonly tend to show a reduced number of scales and other segmental structures (Hubbs, 1918, 1921, 1925, 1926, 1927, 1934, 1940, 1941*a* and *b;* Hubbs and Kuhne, 1937).

TABLE I

RELATIVE NUMBER OF HYBRIDS, *Catostomus commersonnii sucklii* × *Catostomus catostomus griseus,* AND OF THE PARENTAL KINDS

Specimens in University of Michigan Museum of Zoology	*Catostomus commersonnii sucklii*	Hybrids	*Catostomus catostomus griseus*
In collection containing hybrid			
U.M.M.Z. No. 105634	0	1	23
U.M.M.Z. No. 132230	12	1	12
U.M.M.Z. No. 135190	157	3	6
Total	169	5	41
From the Platte River system	1250*	5	692

* Some of these specimens came from localities east of the known range of *C. c. griseus.*

The 5 hybrids between *Catostomus commersonnii sucklii* and *Catostomus catostomus griseus* are essentially intermediate in their ensemble of characters, though in the combined hybrid index (Table XXXIX) one of the specimens closely approaches *sucklii* and one is somewhat more like *griseus* than an exact intermediate. Taking all characters into account, however, it is believed that all 5 specimens are correctly diagnosed as hybrids.

In number of dorsal rays (Table XXXII) the specimens average intermediate, but on this basis alone could not be checked as hybrids since the modal number of rays is only 1 different in the 2 kinds (11 in *sucklii* and 10 in *griseus*). The scale counts (Tables XXXIII to XXXVII) are more diagnostic. The number of transverse rows along the position of the lateral

TABLE II

PROPORTIONATE MEASUREMENTS OF HYBRIDS BETWEEN *Catostomus commersonnii sucklii* AND *Catostomus catostomus griseus*, AND OF THE PARENTAL SPECIES

The measurements are expressed as thousandths of the standard length. There are given for each item the range of the measurements; the average, in parentheses; and, as a subscript, the number of specimens.

	North Platte River, Wyoming and Nebraska			South Platte River, Colorado
Size group, mm.				
C. commersonnii sucklii	32–57 $(44)_{10}$	66–125 $(98)_{7}$	126–182 $(148)_{8}$	77–131 $(103)_{4}$
Hybrids	33–44 $(39)_{2}$	.... $(101)_{1}$	.... $(151)_{1}$	.... $(68)_{1}$
C. catostomus griseus	32–57 $(43)_{9}$	64–113 $(93)_{9}$	127–173 $(144)_{7}$	68–156 $(90)_{10}$
Body depth				
C. commersonnii sucklii	197–215 (204)	193–215 (205)	187–211 (196)	208–225 (216)
Hybrids	203–214 (209)	.... (193)	.... (179)	.... (208)
C. catostomus griseus	167–219 (193)	174–207 (192)	176–200 (190)	172–191 (179)
Caudal peduncle, depth				
C. commersonnii sucklii	82–97 (93)	95–108 (98)	83–96 (89)	92–101 (97)
Hybrids	92–98 (95)	.... (98)	.... (86)	.... (105)
C. catostomus griseus	84–102 (91)	87–107 (96)	75–90 (86)	88–101 (95)
Head length				
C. commersonnii sucklii	279–305 (293)	264–293 (283)	274–297 (283)	254–274 (265)
Hybrids	277–291 (284)	.... (254)	.... (272)	.... (292)
C. catostomus griseus	267–296 (286)	235–272 (258)	227–256 (242)	230–270 (257)
Head depth				
C. commersonnii sucklii	171–182 (178)	155–181 (173)	166–181 (174)	165–174 (171)
Hybrids	157–170 (163)	.... (145)	.... (162)	.... (168)
C. catostomus griseus	153–164 (159)	137–160 (147)	129–148 (135)	129–160 (146)
Head width				
C. commersonnii sucklii	163–175 (168)	155–176 (166)	163–176 (168)	160–177 (167)
Hybrids	152–152 (152)	.... (157)	.... (156)	.... (163)
C. catostomus griseus	142–168 (160)	150–170 (159)	147–162 (153)	146–161 (153)
Snout length				
C. commersonnii sucklii	103–125 (114)	116–136 (126)	121–143 (131)	113–128 (124)
Hybrids	108–109 (109)	.... (123)	.... (126)	.... (131)
C. catostomus griseus	108–122 (116)	108–130 (118)	108–120 (115)	104–124 (112)

TABLE II—(*Cont.*)

	North Platte River, Wyoming and Nebraska			South Platte River, Colorado
Mouth width				
C. commersonnii sucklii	72–85 (77)	67–90 (77)	73–82 (76)	74–90 (83)
Hybrids	82–85 (83)	.... (95)	.... (74)	.... (79)
C. catostomus griseus	82–95 (87)	80–101 (89)	83–98 (92)	78–102 (86)
Cartilaginous ridge, width				
C. commersonnii sucklii	40–48 (42)	39–53 (45)	40–47 (44)	39–44 (41)
Hybrids	45–49 (47)	.... (56)	.... (43)	.... (48)
C. catostomus griseus	49–61 (53)	41–62 (52)	41–53 (47)	49–61 (54)
Mouth length				
C. commersonnii sucklii	51–63 (56)	52–63 (56)	55–63 (58)	53–66 (58)
Hybrids	62–63 (63)	.... (64)	.... (58)	.... (63)
C. catostomus griseus	55–69 (62)	57–71 (63)	60–70 (65)	56–68 (63)
Lower lip, union				
C. commersonnii sucklii	7–18 (11)	13–18 (15)	12–14 (13)	12–13 (13)
Hybrids	9–9 (9)	.... (16)	.... (13)	.... (16)
C. catostomus griseus	11–13 (12)	12–18 (14)	9–17 (14)	13–19 (15)
Dorsal fin to occiput, distance				
C. commersonnii sucklii	240–262 (253)	254–278 (265)	254–284 (273)	262–289 (277)
Hybrids	239–248 (243)	.... (270)	.... (274)	.... (253)
C. catostomus griseus	220–261 (240)	250–299 (270)	284–296 (291)	255–305 (279)
Dorsal fin base				
C. commersonnii sucklii	153–179 (170)	156–178 (166)	153–173 (164)	143–170 (157)
Hybrids	158–161 (159)	.... (153)	.... (148)	.... (184)
C. catostomus griseus	146–172 (159)	133–152 (144)	125–154 (140)	129–155 (141)
Depressed dorsal fin, length				
C. commersonni sucklii	241–271 (255)	252–267 (257)	241–264 (253)	224–269 (246)
Hybrids	235–246 (241)	.... (238)	.... (231)	.... (269)
C. catostomus griseus	234–253 (241)	210–239 (224)	190–222 (211)	199–237 (220)

line is the most critical count, for in this character the 2 parental species are separated by a wide gap, and 4 of the 5 hybrids show no overlap on the range of variation of either.

In the proportionate measurements (Table II) the difference between the parental species is generally slight, and many of the variations overlap widely. It is not surprising, therefore, that in these respects the hybrids show little clear-cut evidence of their mixed parentage. As a whole there is an average tendency toward intermediate proportions. The intermediacy is perhaps best shown, by 4 of the 5 hybrids, in the proportionate length of the depressed dorsal fin.

Better evidence for the hybridity of the 5 specimens comes from other characters (Pl. III, Figs. 1–3). Compared with *C. commersonnii sucklii*, *C. catostomus griseus* has more even contours, less gibbous in the anterior trunk region, less constricted toward the caudal peduncles; the hybrids are in between. The snout of *griseus* is flatter on top than that of *sucklii* and is less decurved in dorsal outline, and it has a much more swollen tip which projects much farther beyond the strictly inferior, rather than somewhat oblique, mouth; in these respects, too, the hybrids are visibly intermediate. In specimens about 100 mm. in standard length the snout of *griseus* is distinctly longer than the postorbital, that of the hybrid is about as long, and that of *sucklii* is definitely shorter than the postorbital. In smaller specimens the snout is relatively shorter in both species and in the hybrids, but the relative distinction holds. Similar intermediate hybrid relations hold for the width of the snout, as measured by the internarial space (Table III).

TABLE III

PROPORTIONATE WIDTH OF SNOUT ON HYBRIDS BETWEEN *Catostomus commersonnii sucklii* AND *Catostomus catostomus griseus*, AND OF THE PARENTAL SPECIES*

Expressed in terms of the internarial distance (between median rims of anterior nostrils) stepped into postorbital length of head (distance from posteroventral rim of eye to free edge of subopercular membrane). Average values, with number of specimens in parentheses.

	Internarial Space in Postorbital Length			
Length groups of specimens	To 50 mm.	50–100 mm.	100–150 mm.	Over 150 mm.
Catostomus commersonnii sucklii	2.0 (12)	1.9 (17)	1.9 (21)	1.8 (8)
Hybrids	1.9 (2)	1.7 (1)	1.6 (1)	1.7 (1)
Catostomus catostomus griseus	1.8 (17)	1.6 (18)	1.4 (19)	1.4 (11)

* These data were obtained too late to be used in the subsequent computations of hybrid intermediacy.

The hybrids are transitional again in the markedly different mouth structures (Pl. II, Figs 2*a–c*). Compared with *sucklii, griseus* has the whole mouth more horizontal, flatter, and more expansive. Both lobes of the lower lip are fuller, therefore with a longer separating incision. The papillae of the lower lip are coarser. The upper lip of *griseus* (approaching that of *Pantosteus*) is somewhat pendant and tends to have an edge separating a relatively smooth outer face from a very coarsely and boldly papillate inner surface; in *sucklii* the upper lip is more strongly and more uniformly swollen and rounded, shows almost no differentiation of an outer and an inner face, and is remarkably uniform in papillation. The cartilaginous ridges or biting edges of the jaws in *griseus* (again approaching *Pantosteus*) are much stronger, and are more transverse and wider than in *sucklii*—in which these ridges are rudimentary. The tangible differences in mouth structure separate *griseus* widely from *sucklii*, leaving a gap into which the hybrids fit.

The 5 specimens also give evidence of hybridity in coloration. The young of *sucklii* have 3 large and rather intense dark blotches along the side of the body, one close to the head, another below the dorsal fin, and the third near the base of the caudal fin (Pl. IV, Fig. 1). These same marks are evident in *griseus* (as in many other suckers), but in that species are smaller and less conspicuous and show a greater tendency to grade into the general dark marbling on the upper sides (which is more prominent than in *sucklii*). In *sucklii* the pattern is less sharply bicolored, for the dark upper parts tend to contrast less markedly and less abruptly with the white lower sides. The individual scale pockets of *sucklii* are usually the more sharply set off, by light centers and by dark-lined borders (Pl. III). All these characters vary with size, but the relative differences persist through most of the life cycle. When the hybrids are compared with specimens of the parent species of like size, the intermediate pigmentation is apparent.

The life colors were also found to be transitional. According to our field notes the half-grown specimen from Laramie River had the dorsal shade of intervening darkness. Intermediacy was also seen in the slight golden tinge of the lower surfaces, and in the slightly yellowish lips. The lower fins had an intermediate amount of red: they were brighter than the pale dirty amber of *sucklii,* duller than the bright orange amber of *griseus.*

Considering all characters, we are convinced by the evidence that *Catostomus commersonnii sucklii* and *Catostomus catostomus griseus* occasionally mate in nature to produce hybrids.

2. *Catostomus macrocheilus* × *Catostomus syncheilus syncheilus*

(Pl. II, Fig. 1*b*; Pl. VI, Fig. 1*b*)

U.M.M.Z. No. 98651: 3 large young 36.5 to 46.5 mm. in standard length, collected by Leonard P. Schultz and Marvin Bowers in sloughs of Wenatchee River at its confluence with Columbia River, near Wenatchee, Chelan County, Washington; August 23, 1932.

U.M.M.Z. No. 98736: 1 young 29 mm. long, seined by Schultz and Bowers in Grande Ronde River in Asotin County, Washington, between Antone, Washington, and Paradise, Oregon; August 29, 1932.

U.M.M.Z. No. 98757: 3 young to half-grown specimens, 35.5, 95, and 113 mm. long, taken by the same collectors in Grande Ronde River 1 mile above Elgin, Union County, Oregon; August 30, 1932.

U.M.M.Z. No. 98761: 3 young 33 to 41 mm. long, obtained on the same expedition in Grande Ronde River at Perry, Union County, Oregon; August 30, 1932.

U.M.M.Z. No. 98776: 37 young 28.5 to 44 mm. in length, seined by Schultz and Bowers in a slough and on the riffles of Umatilla River at Rieth, below Pendleton, Oregon; August 30–31, 1932.

U.M.M.Z. No. 98777: An adult 190 mm. long, taken by the same party in Umatilla River at Echo, Oregon; August 31, 1932.

U.M.M.Z. No. 98793: 7 large young to half-grown, 47.5 to 108 mm. long, secured by Schultz and Bowers in Umatilla River at its confluence with the Columbia; August 31 and September 1, 1932.

U.M.M.Z. No. 130471: 9 yearling and half-grown fish, 60 to 150 mm. in standard length, obtained by Carl L. Hubbs and family in Sucker (= Succor) Creek, a tributary of Snake River, above Rockville, Malheur County, Oregon, about 4 miles from the Idaho line (Town 24 S., Range 46 E.); July 24, 1934.

U.M.M.Z. No. 130482: 1 half-grown of 142 mm., seined on the same trip in Jordan Creek, a tributary of Owyhee River, at Ruby Ranch about midway between Jordan Valley and Rome, Malheur County, Oregon (T. 30 S., R. 44 E.); July 24, 1934.

U.M.M.Z. No. 131787: 1 yearling 35 mm. long, seined by Leonard P. Schultz and Leo Erkkila in Crab Creek 1 mile above Beverly Slough (formed by flood water from the Columbia River); June 19, 1932.

U.M.M.Z. No. 131788: 2 yearlings, 34 and 36 mm. in length, taken by the same collectors in Crab Creek at Smyrna; June 19, 1932.

U.M.M.Z. No. 138616: 1 young 36 mm. long, collected by Stanley G. Jewett, Jr., and Edwin Niska about 1 mile above Umatilla River dam; September 17, 1940. The counts and measurements of this specimen are intermediate, but it was discovered too late for inclusion in the tabulations.

TABLE IV

RELATIVE NUMBERS OF HYBRIDS, *Catostomus macrocheilus* × *Catostomus syncheilus syncheilus*, AND OF THE PARENTAL KINDS

Specimens in University of Michigan Museum of Zoology	*Catostomus macrocheilus*	Hybrids	*Catostomus syncheilus syncheilus*
In collections containing hybrid			
U.M.M.Z. No. 98651	73	3	0
U.M.M.Z. No. 98736	20	1	0
U.M.M.Z. No. 98757	8	3	39
U.M.M.Z. No. 98761	0	3	3
U.M.M.Z. No. 98776	120	37	88
U.M.M.Z. No. 98777	16	1	3
U.M.M.Z. No. 98793	116	7	3
U.M.M.Z. No. 130471	6	9	125
U.M.M.Z. No. 130482	3	1	3
U.M.M.Z. No. 131787	13	1	0
U.M.M.Z. No. 131788	0	2	6
U.M.M.Z. No. 138616	9	1	3
Total	384	69	273
From the Columbia River system	969	69	1341*

* In this total we include all available material of *syncheilus* other than the Palouse River population of *C. syncheilus palousеanus*, though other subspecies are seemingly included.

The failure to get both parental species at 5 of the 12 localities where hybrids were secured is not very surprising. Hybrids Nos. 98651 and 131787 were collected in sloughs where *macrocheilus* but not *syncheilus* would be at home. *Catostomus syncheilus* shows a greater preference for smaller and more rapid waters. *C. macrocheilus* is widespread ecologically, though the adults and many young tend to drop back into quiet pools and bayous. In the spring spawning season both species no doubt seek out gravelly stretches in creeks, as this is the usual spawning locale for suckers in general (Reighard, 1920). Schultz (1941: 28) definitely stated that *C. macrocheilus* "spawns in the spring, usually in April and May, when large numbers migrate up the stream and deposit their eggs on the gravel riffles in swiftly flowing water." The fact that either the one or the other parent species only was taken with hybrids Nos. 98736, 98761, and 131788 may be attributed to chance and to the small size of the collections, for both parental forms occur in similar habitats in the immediate vicinity.

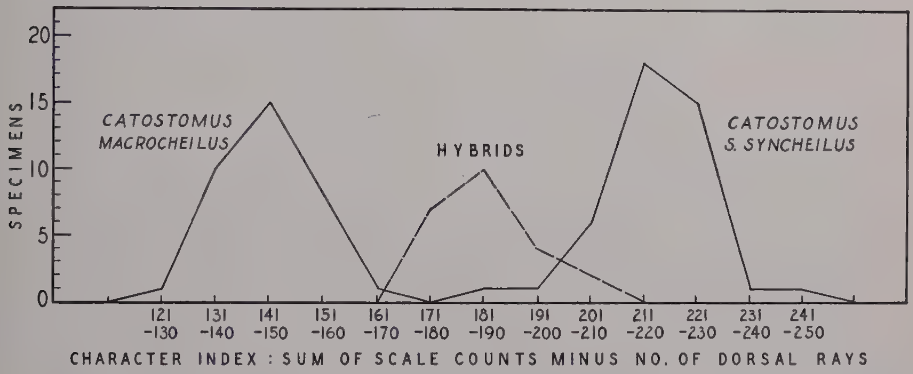

FIG. 1. Comparison of hybrids, *Catostomus macrocheilus* × *Catostomus s. syncheilus*, with the parental species in a character index involving scale and ray counts (Table V).

Until recently the status of the forms of *Catostomus* in the Columbia River system was very much confused, but it now appears clear that 3 species are represented there (Schultz, 1941: 27–30). Of these, *Catostomus catostomus* (as subspecies *pocatello* and either *catostomus* or *griseus*) is largely confined in this drainage basin to the Rocky Mountain region. More widespread are (1) the well-known, coarse-scaled *C. macrocheilus,* and (2) a form long confused with *C. catostomus,* though now known to be quite distinct. This second species is *Catostomus syncheilus* Hubbs and Schultz (1932). The differential features of *C. macrocheilus* and *C. syncheilus* should be kept clearly in mind, for these are obviously the species which hybridize with considerable frequency.

On the average, the hybrid indices for each individual of the *C. macrocheilus* × *C. syncheilus syncheilus* combination show the expected interspecific intermediacy: the average value for the 68 hybrid specimens is 53 (Table XXXIX). Approximately half (33) of the specimens have the index between 45 and 75. The considerable spread is probably to be attributed less to the true variability of the hybrids than to the small size of most of the examples at hand. Probably few if any of the specimens are misjudged to be hybrids, but on account of the small size the differences in proportions are minimized and the counts and measurements are subject to considerable error.

The interposition of the hybrids is again illustrated by the counts. In the number of dorsal rays and in the counts of scales in the several series, the hybrids bridge over the gap between the parental species (Tables XXXII to XXXVII; Fig. 7). There is considerable overlap in each of the comparisons (without, however, a marked increase in variability). The transgression of the hybrid characters on those of the 2 species is almost wholly eliminated when the counts are combined into a character index, similar (but not quite identical) to that used by Schultz and Thompson (1936: 74–75), in the distinction of *Catostomus syncheilus palouseanus*. The index as here used is obtained by adding all the scale counts (which tend to be higher in *syncheilus*) and then subtracting from this sum the dorsal ray count

TABLE V

CHARACTER INDICES (SUM OF ALL SCALE COUNTS MINUS NUMBER OF DORSAL RAYS) IN HYBRIDS BETWEEN *Catostomus macrocheilus* AND *Catostomus syncheilus*, AND IN THE PARENTAL SPECIES

Character Index	Columbia River System (Excluding Palouse Division)			Palouse River System		
	Catostomus macrocheilus	Hybrids	*Catostomus syncheilus syncheilus*	*Catostomus macrocheilus*	Hybrids	*Catostomus syncheilus palouseanus*
121–130	1	....	....	1	....	....
131–140	10	....	....	1	....	....
141–150	15	....	....	15	....	....
151–160	8	....	....	7	....	....
161–170	1	....	....	4	....	....
171–180	....	7	....	1	....	....
181–190	....	10	1	....	1	....
191–200	....	4	1	....	....	1
201–210	....	2	6	....	1	....
211–220	....	....	18	....	....	7
221–230	....	....	15	....	....	7
231–240	....	....	1	....	....	12
241–250	....	....	1	....	....	2
251–260	....	....	....	....	....	1
Specimens*	35	23	43	29	2	30
Average†	145	186	218	150	197	229
Standard error†	1.4	1.8	1.6	1.8	....	2.0
V	5.7	4.6	4.8	6.5	....	4.8

* The number of specimens is lower than in other tables because all of the scale counts could not be taken accurately in some of the smallest fish.

† Computed from the original, unclassed data.

(which tends to be higher in *macrocheilus*). The results, for the 2 *macrocheilus* × *syncheilus* comparisons, are given in Table V and Figure 1. The frequency distribution for the hybrids is unimodal and essentially normal, and again there is no increase in variability.

Similar intermediacy is exhibited by the proportionate measurements (Table VI), though less strikingly than for the counts because of the greater variation and greater overlap in the dimensions. Definite intermediacy for all or nearly all of the comparisons (broken down by locality and by size group) is indicated for the length and depth of the head, the width of the mouth and of the cartilaginous ridge, the length of the union of the lower lip (except in young fish), the distance from the dorsal fin to the occiput, and, particularly well, for the basal length and the depressed length of the dorsal fin. A slight tendency toward intermediacy is shown for the depth of the caudal peduncle. The 4 other measurements (body depth, head width, snout length, and mouth length) are not critical.

As pointed out earlier, hybridity is not demonstrated for a group of specimens by an intermediate average measurement for any part of the body, since a mixture of specimens of the 2 supposed parental species would also yield an intervening average. Hybridization without any clear-cut Mendelian segregation will be indicated when the specimens in question have a unimodal frequency distribution about an intermediate mean. Unequivocal testimony of this sort is difficult to obtain for measured characters, because almost all the proportions vary so much with age and locality that any reasonable units of comparison ordinarily contain too few specimens to show the true nature of the frequency distributions. Inspection of the relatively abundant data for the *C. macrocheilus* × *C. s. syncheilus* cross, however, indicates that the hybrids tend to be intermediate in the proportionate measurements, with a clustering of the values about the intermediate means.

Two of the more significant measurements have been combined into a simple character index to test the frequency distribution of the resulting proportion about the intermediate mean. This index is:

$$\frac{\text{Distance from origin of dorsal fin to occiput}}{\text{Length of depressed dorsal fin}}$$

It is applied to young specimens 25 to 63 mm. in standard length for 2 reasons:

(1) The hybrid nature of small specimens is in special need of confirmation—the hybridity of the larger individuals is more palpably evident.

(2) The index is consistent only in the young. Some of the larger specimens of each group (*macrocheilus,* hybrids, *syncheilus*) have the index about as in the young; others have a smaller fin, giving a higher index. Either sexual dimorphism or a differential attainment of maturity at comparable sizes introduces a complexity. Between the lengths of 25 and 63 mm. analysis shows no significant progressive change in the index. Therefore, the data for this size range only are considered. It is clear from the data (Table VII

TABLE VI

PROPORTIONATE MEASUREMENTS OF HYBRIDS BETWEEN *Catostomus macrocheilus* AND *Catostomus syncheilus syncheilus*, AND OF THE PARENTAL FORMS

The measurements are expressed as thousandths of the standard length. There are given for each item the range of the measurements; the average, in parentheses; and, as a subscript, the number of specimens.

	Umatilla River, Oregon			Wenatchee River and Lower Crab Creek, Washington	Grande Ronde River, Oregon and Washington		Jordan Creek, Oregon	Sucker Creek, Oregon
Size group, mm.								
C. macrocheilus	28–52 (36)$_{30}$	88–110 (97)$_{8}$	128–256 (198)$_{7}$	35–46 (42)$_{10}$	26–38 (32)$_{9}$	102–168 (130)$_{3}$	77–122 (106)$_{3}$	72–149 (102)$_{6}$
Hybrids	28–48 (35)$_{38}$	80–107 (94)$_{6}$	.... (190)$_{1}$	34–46 (39)$_{6}$	29–40 (35)$_{5}$	95–113 (104)$_{2}$	.... (146)$_{1}$	60–150 (93)$_{9}$
C. s. syncheilus	29–44 (36)$_{28}$	72–91 (83)$_{3}$	....	33–36 (34)$_{8}$	25–40 (32)$_{3}$	74–96 (86)$_{10}$	137–173 (161)$_{3}$	59–166 (102)$_{25}$
Body depth								
C. macrocheilus	171–221 (199)	195–225 (216)	184–231 (212)	191–221 (204)	166–212 (193)	196–226 (209)	208–215 (211)	206–227 (215)
Hybrids	174–216 (194)	215–236 (226)	.... (218)	189–217 (201)	180–195 (186)	201–212 (207)	.... (204)	191–233 (211)
C. s. syncheilus	167–210 (194)	205–225 (217)	....	182–223 (200)*	189–198 (194)	191–218 (205)	195–204 (199)	168–229 (198)
Caudal peduncle, depth								
C. macrocheilus	66–76 (71)	65–75 (71)	71–84 (77)	68–77 (75)	67–75 (71)	75–81 (78)	71–79 (75)	71–83 (77)
Hybrids	69–81 (75)	73–78 (75)	.... (81)	63–84 (77)	67–80 (75)	79–79 (79)	.... (77)	76–81 (78)
C. s. syncheilus	67–79 (74)	78–83 (81)	....	69–86 (78)	70–77 (73)	77–83 (81)	78–79 (78)	67–82 (77)
Head length								
C. macrocheilus	259–303 (282)	248–272 (259)	233–261 (249)	261–286 (276)	273–301 (290)	233–240 (237)	246–269 (259)	254–267 (259)
Hybrids	249–294 (272)	236–245 (241)	.... (242)	257–297 (271)	255–283 (270)	232–250 (241)	.... (238)	233–268 (255)
C. s. syncheilus	250–281 (265)	238–242 (239)	....	264–273 (269)	259–268 (265)	240–255 (247)	212–227 (220)	226–259 (244)

* Computations based on measurements of 7 specimens.

Head depth								
C. macrocheilus	150–186 (176)	161–172 (167)	156–169 (162)	169–190 (179)	167–185 (177)	152–153 (153)	164–171 (168)	159–172 (164)
Hybrids	158–184 (171)	151–161 (155)	... (152)	165–186 (174)	166–183 (173)	151–158 (155)	... (146)	145–172 (158)
C. s. syncheilus	159–175 (166)	146–153 (149)	... ...	161–174 (169)	165–178 (170)	151–159 (154)	132–137 (135)	135–162 (150)
Head width								
C. macrocheilus	140–158 (149)	151–163 (156)	151–165 (155)	139–157 (148)	148–168 (156)	145–151 (148)	152–158 (155)	147–162 (152)
Hybrids	137–164 (152)	151–155 (153)	... (145)	148–161 (151)	145–160 (152)	149–154 (151)	... (146)	147–160 (151)
C. s. syncheilus	140–160 (151)	150–157 (154)	... ...	126–146 (140)	142–158 (152)	143–155 (150)	139–144 (142)	141–159 (149)
Snout length								
C. macrocheilus	85–120 (99)	111–121 (115)	96–122 (113)	87–100 (96)	99–112 (103)	109–121 (114)	105–116 (111)	112–132 (119)
Hybrids	75–115 (95)	105–115 (110)	... (118)	87–112 (100)	86–118 (97)	104–109 (107)	... (113)	100–113 (108)
C. s. syncheilus	82–111 (97)	91–119 (104)	... ...	86–101 (93)	86–96 (93)	109–124 (114)	96–106 (102)	96–117 (107)
Mouth width								
C. macrocheilus	57–88 (71)	62–75 (70)	68–80 (76)	61–73 (68)	64–73 (68)	68–73 (70)	68–70 (69)	75–91 (80)
Hybrids	62–85 (74)	71–83 (78)	... (85)	69–81 (74)	68–82 (75)	71–74 (73)	... (69)	79–92 (86)
C. s. syncheilus	66–85 (76)	79–91 (86)	... ...	61–72 (66)*	68–82 (76)	82–103 (94)	76–83 (80)	81–97 (90)
Cartilaginous ridge, width								
C. macrocheilus	30–43 (39)	32–39 (35)	32–41 (35)	35–44 (38)	37–50 (45)	33–44 (39)	35–38 (37)	41–48 (44)
Hybrids	34–50 (44)	41–56 (46)	... (48)	42–51 (44)	41–48 (44)	42–42 (42)	... (47)	40–53 (48)
C. s. syncheilus	41–50 (46)	49–52 (50)	... ...	42–49 (45)	40–49 (43)	46–57 (53)	51–53 (52)	46–60 (55)

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* Computations based on measurements of 7 specimens.

TABLE VI—(*Cont.*)

	Umatilla River, Oregon			Wenatchee River and Lower Crab Creek, Washington	Grande Ronde River, Oregon and Washington		Jordan Creek, Oregon	Sucker Creek, Oregon
Mouth length								
C. macrocheilus	43–62 (54)	48–61 (53)	54–69 (63)	46–54 (50)	46–53 (50)	52–62 (58)	49–60 (55)	61–76 (68)
Hybrids	48–62 (55)	49–60 (55)	...... (66)	48–57 (52)	46–57 (55)	52–56 (54)	...... (59)	61–76 (70)
C. s. syncheilus	42–70 (57)	54–62 (59)	....	47–52 (49)	54–56 (55)	61–66 (63)	54–57 (55)	59–73 (66)
Lower lip, union								
C. macrocheilus	9–16 (12)	9–13 (11)	9–16 (12)	8–12 (10)	7–15 (12)	15–16 (16)	8–11 (9)	15–20 (18)
Hybrids	10–16 (13)	12–26 (17)	...... (19)	8–13 (11)	10–13 (12)	14–18 (16)	...... (17)	17–26 (21)
C. s. syncheilus	10–22 (14)	23–24 (23)	....	10–14 (12)	9–16 (14)	17–30 (23)	22–24 (23)	18–30 (23)
Dorsal fin to occiput, distance								
C. macrocheilus	237–282 (256)	286–316 (304)	307–323 (315)	225–256 (246)	248–267 (255)	289–294 (292)	265–283 (273)	236–299 (261)
Hybrids	246–296 (269)	300–324 (315)	...... (321)	240–270 (255)	243–272 (260)	275–280 (277)	...... (289)	252–290 (275)
C. s. syncheilus	251–316 (276)	318–335 (327)	....	253–275 (266)	264–276 (270)	263–321 (293)	292–309 (302)	264–321 (290)
Dorsal fin base								
C. macrocheilus	195–253 (224)	198–235 (214)	198–215 (207)	219–255 (243)	222–243 (232)	193–211 (200)	227–244 (234)	203–228 (220)
Hybrids	187–228 (205)	184–221 (201)	...... (186)	195–242 (218)	203–241 (213)	193–205 (199)	...... (203)	198–227 (210)
C. s. syncheilus	178–212 (191)	176–186 (182)	....	160–203 (189)	187–219 (201)	172–204 (185)	173–184 (178)	166–212 (193)
Depressed dorsal fin, length								
C. macrocheilus	268–326 (305)	287–305 (293)	273–321 (297)	301–342 (330)	298–328 (314)	284–295 (290)	330–343 (335)	290–328 (318)
Hybrids	274–315 (292)	268–304 (281)	...... (271)	291–330 (310)	280–330 (296)	284–298 (291)	...... (294)	296–322 (311)
C. s. syncheilus	258–293 (278)	261–269 (266)	....	255–302 (279)	278–291 (283)	255–285 (275)	257–280 (265)	246–315 (289)

and Fig. 2) that the indices for hybrids have an intervening mean, have the same order of variability, and form an approximately normal unimodal frequency distribution. Their identification as hybrids is confirmed and no simple Mendelian segregation is suggested. The data for other measurements, though analyzed in less detail, seem to show the same sort of statistics; as do the dorsal-ray and scale counts (compare Table VII with Tables XXXII to XXXVII).

A further confirmation of the hybrid interpretation is provided by the pelvic-ray count—a character discovered after the paper was written. Again we note intermediacy with no increase in variability (Table VIII).

The intermediacy of the hybrids is well shown also in characters that are not so readily analyzed as are the counts and the ordinary proportions.

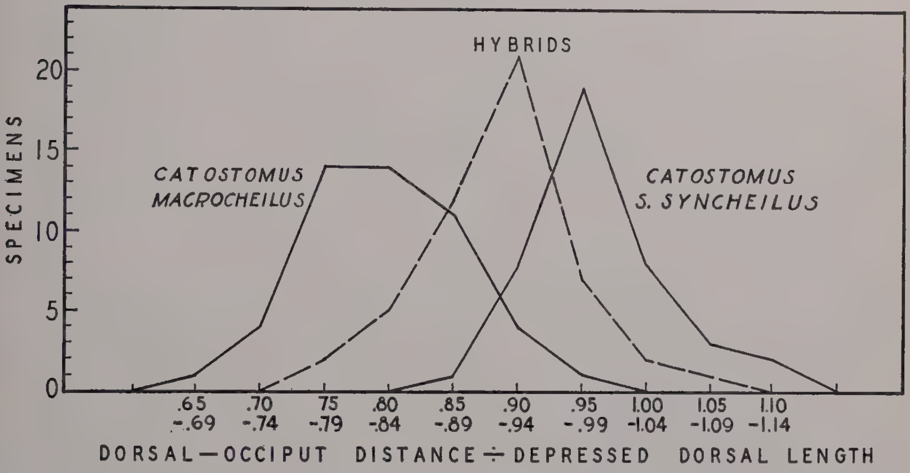

FIG. 2. Comparison of hybrids, *Catostomus macrocheilus* × *Catostomus s. syncheilus*, with the parental species in the ratio of the dorsal–occiput distance to the depressed dorsal length (Table VII).

Thus the snout tends to be less depressed and less prominently projecting beyond the mouth than in *syncheilus*, but more so than in *macrocheilus;* the hybrids tend to be intermediate (Pl. VI, Figs. 1*a*–*c*).

As in most sucker hybrids, the mouth structures also exhibit intermediate characters (as shown in Pl. II, Figs. 1*a*–*c;* compare also Figs. 2*a*–*c* on Pl. VI). The intermediacy is shown in every one of the following features, by which the lips of *syncheilus* differ from those of *macrocheilus:*

1. The lips are broader and flatter.
2. The upper lip is less gibbous and more pendant, especially around the front of the mouth. It has a definite edge (scarcely represented in *macrocheilus*), which separates an outer nearly smooth face from an inner strongly papillate one. In *macrocheilus* there is only an incipient differentiation of this sort.

TABLE VII

FREQUENCY DISTRIBUTION OF THE RATIO OF THE DISTANCE FROM THE ORIGIN OF THE DORSAL TO THE OCCIPUT, TO THE LENGTH OF THE DEPRESSED DORSAL FIN, IN HYBRIDS BETWEEN *Catostomus macrocheilus* AND *Catostomus syncheilus syncheilus*, AND IN THE PARENTAL KINDS

Measured in young specimens, 25 to 63 mm. in standard length.

	Dorsal to Occiput ÷ Depressed Dorsal Length									
	0.65–0.69	0.70–0.74	0.75–0.79	0.80–0.84	0.85–0.89	0.90–0.94	0.95–0.99	1.00–1.04	1.05–1.09	1.10–1.14
C. macrocheilus	1	4	14	14	11	4	1	......	......	......
Hybrids	......	......	2	5	12	21	7	2	1	......
C. s. syncheilus	......	......	......	......	1	8	19	8	3	2

	Statistical Computations					
	No.	Range	Ave.*	S.E.*	V	Hybrid Index with Standard Error
C. macrocheilus	49	0.66–0.97	0.82	.009	7.7	....
Hybrids	50	0.79–1.02	0.91	.008	6.4	56 ± 6
C. s. syncheilus	41	0.88–1.12	0.98	.008	5.4	....

* The averages and standard errors were computed from the original unclassed data.

TABLE VIII

NUMBER OF PELVIC RAYS IN HYBRIDS BETWEEN *Catostomus macrocheilus* AND *Catostomus syncheilus*, AND IN THE PARENTAL SPECIES*

Region and Kind	Number of Rays in Both Pelvic Fins						
	18	19	20	21	22	23	24
Exclusive of Palouse River system							
C. macrocheilus	......	......	7	12	64	6	4
Hybrids	......	1	21	12	28	2	......
C. s. syncheilus	2	7	42	26	31	......	1
Palouse River system							
C. macrocheilus	......	1	1	4	31	4	7
Hybrids	......	......	1	2	......	......	......
C. s. palouseanus	1	2	27	11	14	......	......

	Statistical Computations				
	No.	Ave.	S.E.	V	Hybrid Index ± S.E.$_I$
Exclusive of Palouse River system					
C. macrocheilus	93	21.87	.11	4.9	....
Hybrids	64	21.14	.12	4.6	65 ± 14
C. s. syncheilus	109	20.74	.10	5.1	....
Palouse River system					
C. macrocheilus	48	22.19	.14	4.5	....
Hybrids	3	20.67?	.33?	2.3?	98?
C. s. palouseanus	55	20.64	.13	4.65	....

* These data were obtained too late to be used in the subsequent computations of hybrid intermediacy.

3. At the outer angle of the mouth where the 2 lips are joined, a slight to moderately deep indentation is often developed, at the end of a crease between the upper and lower lips (this feature is hardly shown by the specimen drawn for Fig. 1*c*, Pl. II). In *macrocheilus* this groove is less well developed and does not reach the edge of the mouth, and there is no emargination at the angle.

4. The median incision between the lobes of the lower lips is less developed. The 2 halves of the lip are connected by a flatter and broader isthmus, across which there pass 2 to 5 instead of 1 to 2 rows of papillae.

5. The cartilaginous ridges of the mouth are much more strongly developed, wider, and less curved (more nearly transverse). This development approaches that of *Pantosteus*, but is much less extreme.

Similar intermediacy is exhibited in the coloration. *Catostomus syncheilus* is darker than *macrocheilus.* The fine dark mottlings of the upper parts tend to be more prominent. The dark color usually extends farther down across the lower sides and tends to grade into the light lower surface, rather than to give way somewhat abruptly to a light ventrolateral area on the head and body. In all these respects the hybrids tend to be transitional between the parental species.

A few specimens which we have interpreted as hybrids, particularly in the collections of young, may well belong to either the one or the other of the parental species, and a few diagnosed as the pure species may be hybrids. Most of the determinations, however, seem correct.

We conclude that *Catostomus macrocheilus* and *Catostomus syncheilus syncheilus* hybridize rather commonly. A rather uniform intermediacy pervades all the known distinguishing features: number of dorsal and of pelvic fin rays; number and size of scales on all parts of the body; differences in proportions and form; distinctive characters in the structure of the mouth; differences in coloration. The intermediacy in any one of these systems would suggest hybridization; the intermediacy in all respects virtually clinches the conclusion. By any other theory it would be difficult to explain why the specimens intermediate in counts (Fig. 1) should also show intervening proportions (Fig. 2). The multiple-factor type of inheritance is indicated for all the systematic differentiae.

3. *Catostomus macrocheilus* × *Catostomus syncheilus palouseanus*

(Pl. VI, Fig. 2*b*)

U.M.M.Z. No. 98709: 1 yearling 65 mm. and 1 adult 204 mm. in standard length, seined by Leonard P. Schultz and Marvin Bowers in South Fork of Palouse River, 0.5 mile above Pullman, Washington; August 27, 1932.

U.M.M.Z. No. 98725: 1 young fish 29 mm. long taken by the same collectors on the following day in the Palouse River at Palouse, Washington.

In considering the relative numbers of hybrids and parental species in this combination, and in that of *C. macrocheilus* × *C. s. syncheilus*, it should be recalled that parts of the collections made by Leonard P. Schultz and assistants were retained at the University of Washington.

The interpretation of 3 individuals as hybrids between *C. macrocheilus* and *C. syncheilus palouseanus* is on the same basis as the identification of 69 specimens as hybrids between *macrocheilus* and the typical subspecies of *syncheilus.*

We have found in the Cyprinidae, Poeciliidae, and other families that the hybrids in the same interspecific combination differ, when different subspecies of one (or both) parental species are involved. The difference is in the expected direction, on the assumption that the heterozygotic forms tend to be more or less precisely intermediate between the particular parental types. When a subspecies of a parental species has some peculiarity in counts, measurements, or color, this feature is generally to be seen, in diluted form, in the hybrid. This circumstance is part of the large body of data which convinces us of the validity of the assumption that species of fish hybridize in nature.

TABLE IX

Relative Numbers of Hybrids, *Catostomus macrocheilus* × *Catostomus syncheilus palouseanus*, and of the Parental Kinds

Specimens in University of Michigan Museum of Zoology	*Catostomus macrocheilus*	Hybrids	*Catostomus syncheilus palouseanus*
In collections containing hybrid			
U.M.M.Z. No. 98709	72	2	57
U.M.M.Z. No. 98725	21	1	3
Total	93	3	60
From the Palouse River system	152	3	358

These conclusions are confirmed by the limited data on the hybrids involving *C. s. palouseanus;* unfortunately only 3 specimens have been identified and 1 of these is too small for the determination of some characters. As compared with the hybrids between *C. macrocheilus* and typical *C. s. syncheilus,* those between *C. macrocheilus* and *C. s. palouseanus* have a lower average number of dorsal rays, and a higher average number of scales; *palouseanus* differs from typical *syncheilus* in the same way (as first shown by Schultz and Thompson, 1936), and the Palouse River race of *C. macrocheilus* seems to show a local variation parallel to that exhibited by *C. s. palouseanus.* These relations are perhaps brought out best by the character index involving dorsal ray and scale counts (Table V).

That the 3 hybrids of this combination are nicely intermediate is indicated by their average hybrid indices (Table XXXIX) of 50, 57, and 60, on the percentage scale in which 50 denotes exact intermediacy in all the characters studied.

TABLE X

PROPORTIONATE MEASUREMENTS OF HYBRIDS BETWEEN *Catostomus macrocheilus* AND *Catostomus syncheilus palouseanus*, AND OF THE PARENTAL SPECIES

The measurements are expressed as thousandths of the standard length. There are given for each item the range of the measurements; the average, in parentheses; and, as a subscript, the number of specimens.

	Palouse River System, Washington		
Size group, mm.			
C. macrocheilus	30–42 (36)$_{25}$	44–105 (80)$_{18}$	120–255 (195)$_{7}$
Hybrids	.... (29)$_{1}$	.... (65)$_{1}$	.... (204)$_{1}$
C. syncheilus palouseanus	33–40 (36)$_{13}$	44–85 (65)$_{14}$	122–178 (140)$_{15}$
Body depth			
C. macrocheilus	177–215 (197)	189–236 (213)	203–221 (213)
Hybrids	.... (207)	.... (198)	.... (198)
C. syncheilus palouseanus	186–243 (221)	183–247 (219)	193–217 (205)*
Caudal peduncle, depth			
C. macrocheilus	65–79 (74)	68–81 (73)	72–83 (79)
Hybrids	.... (90)	.... (79)	.... (79)
C. syncheilus palouseanus	71–86 (81)	77–84 (81)	75–86 (81)
Head length			
C. macrocheilus	271–306 (287)	254–286 (269)	244–265 (253)
Hybrids	.... (274)	.... (274)	.... (243)
C. syncheilus palouseanus	252–275 (266)	232–270 (251)	218–254 (231)
Head depth			
C. macrocheilus	173–188 (181)	162–181 (173)	163–172 (167)
Hybrids	.... (176)	.... (166)	.... (150)
C. syncheilus palouseanus	161–182 (169)	153–176 (160)	134–155 (143)
Head width			
C. macrocheilus	148–164 (156)	145–164 (156)	154–169 (162)
Hybrids	.... (159)	.... (173)	.... (163)
C. syncheilus palouseanus	142–166 (157)	136–164 (151)	145–166 (152)
Snout length			
C. macrocheilus	91–122 (109)	95–131 (120)	112–141 (131)
Hybrids	.... (99)	.... (114)	.... (125)
C. syncheilus palouseanus	94–115 (104)	93–118 (108)	91–123 (113)

* Computations based on measurements of 14 specimens.

TABLE X—(*Cont.*)

PROPORTIONATE MEASUREMENTS OF HYBRIDS BETWEEN *Catostomus macrocheilus* AND *Catostomus syncheilus palouseanus*, AND OF THE PARENTAL SPECIES

	Palouse River System, Washington		
Mouth width			
C. macrocheilus	68–85 (75)	64–83 (76)	67–102 (85)
Hybrids	.... (77)	.... (91)	.... (78)
C. syncheilus palouseanus	73–92 (80)	73–104 (86)	81–107 (94)
Cartilaginous ridge, width			
C. macrocheilus	38–55 (42)	36–44 (40)	35–46 (41)
Hybrids	.... (50)	.... (48)	.... (43)
C. syncheilus palouseanus	31–46 (43)	40–57 (49)	45–57 (51)
Mouth length			
C. macrocheilus	47–65 (55)	51–64 (58)	57–77 (70)
Hybrids	.... (55)	.... (65)	.... (60)
C. syncheilus palouseanus	52–60 (56)	47–75 (61)	64–77 (69)
Lower lip, union			
C. macrocheilus	8–17 (12)*	9–16 (12)	13–20 (15)
Hybrids	.... (17)	.... (17)	.... (17)
C. syncheilus palouseanus	11–19 (17)	15–25 (19)†	16–30 (23)
Dorsal fin to occiput, distance			
C. macrocheilus	235–264 (250)	233–276 (256)	250–300 (282)
Hybrids	.... (227)	.... (266)	.... (287)
C. syncheilus palouseanus	244–272 (261)	263–292 (279)	251–320 (284)
Dorsal fin base			
C. macrocheilus	184–237 (215)	192–242 (215)	179–212 (190)
Hybrids	.... (197)	.... (186)	.... (176)
C. syncheilus palouseanus	182–208 (191)	169–222 (187)	156–199 (178)
Depressed dorsal fin, length			
C. macrocheilus	282–327 (302)	281–332 (301)	252–298 (272)
Hybrids	.... (286)	.... (281)	.... (248)
C. syncheilus palouseanus	259–294 (275)	255–293 (274)†	221–304 (264)

* Computations based on measurements of 24 specimens.

† Computations based on measurements of 13 specimens.

The intermediate features of *C. macrocheilus* × *C. syncheilus palouseanus* hybrids involve proportionate measurements as well as the counts. As shown by Table X, either 2 or all of the 3 hybrids are intermediate between specimens of the parental types of comparable sizes in: the length and depth of the head, the length of snout, the width of the cartilaginous ridge in the mouth, the length of the union of the lower lip (Pl. VI, Figs. 2*a*–*c*), and the length of the depressed dorsal fin. Inconsistent results were obtained for the depth of the body and of the caudal peduncle, the width of the head and of the mouth, the distance between the origin of the dorsal fin and the occiput, and the length of the base of the dorsal fin.

The interpretation of hybrid origin and of the seemingly Galtonian inheritance of the systematic characters is confirmed by the form of the snout, the structure of the mouth, and the coloration (Pl. VI, Figs. 2*a*–*c*). The remarks on these features given for the *C. macrocheilus* × *C. s. syncheilus* cross apply *in toto*.

HYBRIDS BETWEEN THE GENERA *CATOSTOMUS* AND *PANTOSTEUS*

With even greater confidence we can claim that species of *Catostomus* and of *Pantosteus* hybridize in nature. In these combinations, intergeneric according to the current nomenclature of the family, the gap between the parental species is so wide and involves so many characters that specimens which are intermediate in all important respects can hardly be interpreted in any other light. Many of the differences which distinguish *C. catostomus* from *C. commersonnii*, and *C. syncheilus* from *C. macrocheilus* appear exaggerated when we contrast species of *Pantosteus* with those of *Catostomus*. The snout of *Pantosteus* is much more depressed and bulbous and projects beyond the mouth (Pls. IV to VII). The upper lip (Pls. I and IV) in *Pantosteus* is even more modified than in *Catostomus catostomus* and *C. syncheilus*, in the better developed ridge and in the overhanging form, with the smoother outer part tending to overlap the strongly papillate inner surface. The lips are flatter. The crease separating the upper and lower lips on each side is deeper and extends to the angle of the rather deep emargination at the outer corner of the mouth. On the midline, in contrast, the lower lips are much more broadly conjoined. The cartilaginous biting or scraping edge of the lower jaw is much better developed. This ridge is stronger, broader, and much more nearly transverse. The gape in consequence is straightish, rather than strongly arched. The outer ends of the ridge are more definitely shouldered. In some species of *Catostomus*, notably *C. commersonnii*, the mouth is moderately oblique, whereas in *Pantosteus* it is always strictly inferior and horizontal (Pls. IV–V). In *Pantosteus* the general color is darker, and the peritoneum is more jet-black than in the species of *Catostomus* with which it has been found to hybridize (the differences in peritoneal pigment are especially notable in the young, in which the black color often shows through the thin belly wall). The intestine averages longer, and the air bladder more reduced in size.

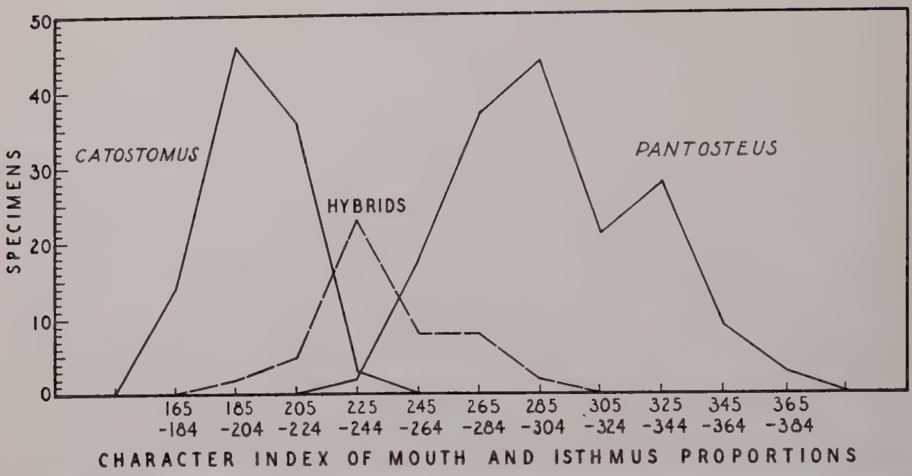

FIG. 3. Comparison of all *Catostomus* × *Pantosteus* hybrids with the parental species in the character index of mouth and isthmus proportions.

The concordant data of 1942 for the *Catostomus*, species × *Pantosteus santa-anae* cross are included in Tables XI and XII, but not in this graph.

In all these respects the hybrids correspond with neither parent species, but are intermedial. The hybrids of the different *Catostomus* × *Pantosteus* combinations are not exactly alike, nor would this be expected, for the parental species of the several combinations are diverse. Thus in mouth structure the special features of the parent species of the different combinations are reflected by the hybrids (Pls. I and IV).

That the mouths of the *Catostomus* × *Pantosteus* hybrids are intermediate in measurements as well as in structural details is brought out by the data in Tables XI and XII and in Figures 3 and 4. In order to restrict the overlap of the hybrid values on those of the parental types and to simplify

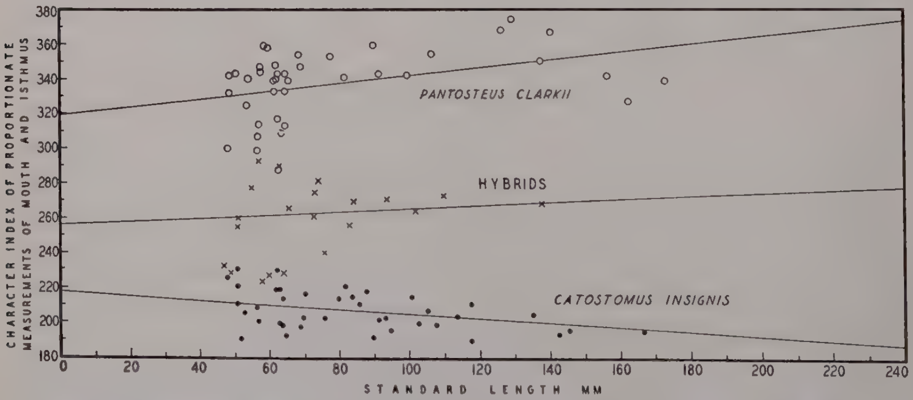

FIG. 4. Variation with standard length of the character index involving mouth and isthmus proportions in hybrids, *Catostomus insignis* × *Pantosteus clarkii*, and in the parental species.

TABLE XI

Frequency Distribution, in *Catostomus* × *Pantosteus* Hybrids, of the Character Index of Mouth and Isthmus Measurements

The index represents the sum of the proportionate measurements, expressed in thousandths of the standard length, of (1) the width of the mouth, (2) the width of the cartilaginous ridge of the mouth, (3) the length of the union of the lower lip, and (4) the width of the isthmus.

	Character Index Frequencies											Statistical Computations					
	165–184	185–204	205–224	225–244	245–264	265–284	285–304	305–324	325–344	345–364	365–384	No.	Range	Ave.	S.E.	V	Hybrid Index
C. c. sucklii	4	5	1	......	......	......	......	......	......	......	......	10	177–205	189	2.8	4.7	......
Hybrids	......	......	......	2	......	......	......	......	......	......	......	2	239–244	241	......	......	46
P. jordani	......	......	......	......	......	......	6	4	......	......	......	10	285–316	301	3.0	3.15	......
C. c. sucklii	1	6	......	......	......	......	......	......	......	......	......	7	181–202	190	2.6	3.6	......
Hybrids	......	2*	2	3	......	......	......	......	......	......	......	7	187–232	215	7.0	8.6	25
P. d. delphinus	......	......	......	......	5	6	6	3	4	1	......	25	245–360	291	6.1	10.5	......
C. insignis	......	21	16	3	......	......	......	......	......	......	......	40	190–231	206	1.7	5.2	......
Hybrids	......	......	1	5	5	8	2	......	......	......	......	21	224–293	259	4.6	8.1	40
P. clarkii	......	......	......	......	......	......	3	5	19	10	3	40	288–374	338	3.0	5.6	......
Catostomus, sp.	3	1	......	......	......	......	......	......	......	......	......	4	168–195	177	6.0	5.9	......
Hybrids	......	1	20	21	2	......	......	......	......	......	......	44	200–251	226	1.7	5.0	47
P. santa-anae	......	......	......	1	6	20	16	3	......	......	......	46	244–324	282	2.5	6.0	......
C. tahoensis	7	11	4	......	......	......	......	......	......	......	......	22	166–218	191	2.8	6.9	......
Hybrids	......	......	1	8	1	......	......	......	......	......	......	10	212–254	233	3.5	4.75	40
P. lahontan	......	......	......	1	5	12	12	3	3	......	......	36	233–339	295	3.9	7.9	......
C. c. griseus	......	1	11	......	......	......	......	......	......	......	......	12	204–220	211	1.6	2.6	......
Hybrid	......	......	......	......	1	......	......	......	......	......	......	1	245	245	......	......	40
P. jordani	......	......	......	......	1	2	4	3	1	......	......	11	262–343	297	6.6	7.4	......
C. l. discobolus	......	1	4	......	......	......	......	......	......	......	......	5	194–221	210	4.5	4.8	......
Hybrid	......	......	......	1	......	......	......	......	......	......	......	1	231	231	......	......	23
P. d. utahensis	......	......	......	......	1	......	1	2	1	......	......	5	251–331	301	13.8	10.25	......
Totals:																	
Catostomus	15	46	36	3	......	......	......	......	......	......	......	100	166–231	200	1.5	7.5	......
Hybrids	......	3	24	40	9	8	2	......	......	......	......	86	187–293	235	2.2	8.8	42†
Pantosteus	......	......	......	2	18	40	48	23	28	11	3	173	233–374	302	2.4	15.4	......

* These low values for the character index are probably attributable to the small size of the 2 specimens (34 and 42.5 mm.)

† Grand average of all the individual hybrid indices.

the comparisons, we have united into 1 character index the 3 proportional measurements of the mouth that tend to be higher in *Pantosteus* than in *Catostomus,* namely, the over-all width, the width of the cartilaginous ridge of the mandible, and the length of the union of the lower lip; and for further distinctiveness of the index, we have added the proportionate width of the isthmus, which also tends to have a high value in *Pantosteus.* One reason for such a combination of proportionate measurements is to give joint expression to a series of characters and to minimize the importance of extreme fluctuations in single features. These object~~ions~~s have been so well attained in the present application of the character index that it is possible to combine the indices for all localities and size groups of each combination without confusing the picture. Inspection of the frequency table indicates that the character indices of the hybrids overlap relatively little on those for the parental species, and a scrutiny of the raw data shows that perhaps half of this moderate overlap is attributable to age and local variation rather than to individual variation. Obviously, the hybrids have values for this index of mouth and isthmus dimensions that intervene between the usual figures for the parental species. Again the frequency distribution is unimodal, and apparently of essentially the normal type.

TABLE XII

FREQUENCY DISTRIBUTION OF THE HYBRID INDEX DERIVED FROM THE CHARACTER INDEX OF MOUTH AND ISTHMUS DIMENSIONS, FOR ALL *Catostomus* × *Pantosteus* HYBRIDS

Hybrid Index								Statistical Computations			
−5.1 to 5.0	5.1 to 15.0	15.1 to 25.0	25.1 to 35.0	35.1 to 45.0	45.1 to 55.0	55.1 to 65.0	65.1 to 75.0	No.	Range	Ave.	S.E.
1*	2*	9	4	32	24	11	3	86	−3 to 70	42	1.5

* The 2 very low values (−3 and 6) are due in part at least to the small size of the specimens (see footnote to Table XI); all other indices ranged from 14 to 70.

The relative growth of the lips and isthmus as combined into the character index seems to be intermediate in the hybrid: the index value increases with age in *Pantosteus clarkii,* remains nearly level in the hybrids, and decreases with age in *Catostomus insignis* (Fig. 4).

In this character index most of the hybrids, for some reason, approach the *Catostomus* parent somewhat more closely than they do the *Pantosteus* species involved in the cross. This relation is best brought out by computing, for each individual hybrid in each combination, the hybrid index (pp. 6–8), and then averaging the 86 indices—as done in Table XII. In each measurement involved in the computation of this hybrid index the hybrids tend to resemble the *Catostomus* parent the more closely; that is, the hybrid indices average lower than 50 (Table XXXVIII).

The species of *Pantosteus* usually have shorter dorsal fins, with fewer rays on the average, than do the forms of *Catostomus;* and the hybrids have intervening average numbers. This is indicated for 6 of the 7 combinations (Table XXXII). In the 1 exceptional case the parental types are very close, and there are only 2 hybrid specimens.

The interjacence of these intergeneric hybrids is well shown by the scale counts (Tables XXXIII to XXXVII). The hybrids tend to be intermediate in scale number whether the *Pantosteus* parent-form has fewer scales or more scales than the *Catostomus* species entering the cross.

It seems superfluous to compare all the intergeneric hybrids in detail with their respective parental species. There can be little doubt of the interpretations, except possibly for an occasional specimen. The hybrids show intermediacy not only in the characters in which the genera differ. They have values which interpose between those of the particular species of the 2 genera which occur in the same place.

Since 2 species of *Pantosteus* seldom if ever occur together, and since the species of *Catostomus* which here and there occur together are very distinct, we have felt little hesitancy in our interpretations of the species which are involved in each of the intergeneric crosses.

4. *Catostomus commersonnii sucklii* × *Pantosteus jordani*

(Pl. IV, Fig. 2)

U.M.M.Z. No. 120375: 1 half-grown 56 mm. long to caudal base, captured by L. C. Stuart and A. M. Stebler in Grace Coolidge Creek about 1 mile above State Game Lodge, Custer State Park, Custer County, South Dakota; August 7, 1934.

U.M.M.Z. No. 120381: 1 half-grown 57 mm. long, collected by L. C. Stuart in French Creek above the new dam about 5 miles east of Custer, Custer County, South Dakota; August 27, 1934.

TABLE XIII

RELATIVE NUMBERS OF HYBRIDS, *Catostomus commersonnii sucklii* × *Pantosteus jordani*, AND OF THE PARENTAL SPECIES

Specimens in University of Michigan Museum of Zoology	*Catostomus commersonnii sucklii*	Hybrids	*Pantosteus jordani*
In collection containing hybrid			
U.M.M.Z. No. 120375	14	1	37
U.M.M.Z. No. 120381	33	1	7
Total	47	2	44
From the Missouri River system	2111*	2	691

* Including a few specimens from the eastern part of the Missouri River system which may be referable to *C. c. commersonnii.* A considerable percentage of the *C. c. sucklii* total represents specimens from beyond the known range of *Pantosteus.*

These 2 sucker specimens can hardly represent any known or unknown species, for they are very distinctive in characters and come from the rather thoroughly collected region of the Black Hills. They obviously are hybrids

TABLE XIV

PROPORTIONATE MEASUREMENTS OF HYBRIDS BETWEEN *Catostomus commersonnii sucklii* AND *Pantosteus jordani*, AND OF THE PARENTAL SPECIES

The measurements are expressed as thousandths of the standard length. There are given for each item the range of the measurements; the average, in parentheses; and, as a subscript, the number of specimens.

French and Grace Coolidge Creeks, South Dakota

Size group, mm.		Snout length	
C. commersonnii sucklii	50–70 $(62)_{10}$	*C. commersonni sucklii*	108–130 (121)
Hybrids	56–57 $(57)_{2}$	Hybrids	107–128 (117)
P. jordani	48–79 $(55)_{10}$	*P. jordani*	104–120 (110)
Caudal peduncle, depth		Mouth width	
C. commersonnii sucklii	85–94 (88)	*C. commersonnii sucklii*	74–86 (79)
Hybrids	85–89 (87)	Hybrids	94–102 (98)
P. jordani	78–91 (83)	*P. jordani*	102–115 (108)
Head length		Cartilaginous ridge, width	
C. commersonnii sucklii	284–301 (294)	*C. commersonnii sucklii*	36–44 (40)
Hybrids	267–281 (274)	Hybrids	47–48 (47)
P. jordani	243–265 (254)	*P. jordani*	62–69 (65)
Head depth		Mouth length	
C. commersonnii sucklii	168–182 (176)	*C. commersonnii sucklii*	53–62 (56)
Hybrids	165–167 (166)	Hybrids	65–68 (67)
P. jordani	143–160 (151)	*P. jordani*	63–78 (69)
Head width		Lower lip, union	
C. commersonnii sucklii	164–178 (169)	*C. commersonnii sucklii*	10–16 (14)
Hybrids	163–168 (165)	Hybrids	16–21 (19)
P. jordani	150–165 (158)	*P. jordani*	27–38 (32)
Isthmus width			
C. commersonnii sucklii	52–62 (55)		
Hybrids	73–82 (77)		
P. jordani	87–102 (96)		

between the 2 common species of the region. No other kind of either *Catostomus* or *Pantosteus* occurs there. They show intermediate values, or averages, for the:

Number of dorsal rays (Table XXXII),

Number of scales in all 5 series counted (Tables XXXIII to XXXVII),

Length, depth, and width of head; width of isthmus; length of snout; and the several mouth measurements (Table XIV),

Form of snout, structure and slant of mouth, coloration, etc. (as indicated on pp. 33–36; Pl. IV).

The average hybrid indices for the 2 specimens are respectively 39 and 48 (Table XXXIX).

5. *Catostomus commersonnii sucklii* × *Pantosteus delphinus delphinus*

(Pl. V, Fig. 2)

U.M.M.Z. No. 105638: 5 young and yearling specimens 34 to 74.5 mm. in standard length, seined by W. Petravicz and Middendorf in Colorado River, near its headwaters, at Hot Sulphur Springs, Grand County, Colorado; July 28, 1938.

U.M.M.Z. No. 136912: 1 half-grown 128 mm. and 1 adult 231 mm. long, collected by John Greenbank in Dry Creek, a tributary of Gunnison River, 3 miles west of Olathe, Montrose County, Colorado; April 21, 1941.

TABLE XV

Relative Numbers of Hybrids, *Catostomus commersonnii sucklii* × *Pantosteus delphinus delphinus*, and of the Parental Species

Specimens in University of Michigan Museum of Zoology	*Catostomus commersonnii sucklii*	Hybrids	*Pantosteus delphinus delphinus*
In collections containing hybrid			
U.M.M.Z. No. 105638	0	5	23
U.M.M.Z. No. 136912	1	2	11
Total	1	7	34
From the Colorado River system	10	7	2031*

* Many of these are from areas into which *C. c. sucklii* has not yet spread, or were collected prior to the introduction of that species.

The most exceptional and unexpected conditions under which these hybrids were obtained are explained on pp. 12–13. The very high frequency of the hybrids in comparison with the number of specimens of *Catostomus commersonnii sucklii* known from the Colorado River system is probably attributable to the recent introduction of that species into the Colorado River drainage. Such disruptions of long-standing ecological relationships apparently favor hybridization. The incidence of interspecific mating has presumably been increased by the scarcity of the introduced form and the abundance of the native *Pantosteus d. delphinus* at the times and places of collecting. The *sucklii* strays have probably found it as easy to contact spawning schools of *delphinus* as to establish pure spawning runs in an area already saturated with sucker populations.

The characters of these hybrids, at least on the average, are intercalated rather well between those of the parental species. This is true of the:

Number of dorsal rays (Table XXXII),
Number of scales in all 5 series counted (Tables XXXIII to XXXVII),
Depth of caudal peduncle (slender in *P. d. delphinus,* Pl. V), depth of head, width of isthmus, length of snout (in No. 105638 only), and in all dimensions of the mouth and lips (Table XVI). The length and the width of the head are the only noncommittal characters. Some of these characters are shown on the figures (Pl. V, Figs. 1–3).

It was first thought that the 2 specimens, No. 136912, might be hybrids between *Catostomus commersonnii sucklii* and *C. latipinnis discobolus,* but the measurements fitted that assumption very poorly, and a more detailed examination of the mouth disclosed *Pantosteus*-approaching features. The size of the scales further indicates that the called-for *Catostomus* parental species is neither the native *C. l. discobolus* nor *C. catostomus griseus,* which Mr. Greenbank also collected in the region. Particularly impressive is the approach shown by the hybrids to the peculiar squamational pattern of *P. d. delphinus,* which has very small scales forward but large ones in the caudal region (Pl. V).

Some of the 7 specimens approach the *Catostomus* parental species, others are closer to the *Pantosteus* form. The hybrid indices grade from 28 to 85, with an average of 53, close to the midpoint (Table XXXIX).

6. *Catostomus insignis* × *Pantosteus clarkii*

(Pl. I, Fig. 3*b*; Pl. VI, Fig. 3*b*)

U.M.M.Z. No. 110433: 1 half-grown 110 mm. in length to base of caudal fin, seined by C. M. Tarzwell in Taylor Creek, near the road between Beaverhead and Silver City, Gila National Forest, New Mexico; August 16, 1935.

U.M.M.Z. No. 118175: 3 young to half-grown 51 to 138 mm. long, taken by Gee and Carr of the U. S. Forest Service in Taylor Creek, New Mexico; August 26, 1937.

U.M.M.Z. No. 121642: 6 yearlings 73 to 94 mm. in length, seined by Tarzwell and Smith in the Middle Fork of the East Branch of Black River, at Crosby Ranch, Apache National Forest (Town 6 N., Range 28 E.), Arizona; July 22, 1937.

U.M.M.Z. No. 121646: 1 half-grown of 102 mm., taken by the same collectors in the West Fork of the East Branch of Black River at Three Forks, Apache National Forest (T. 5 N., R. 29 E.), Arizona; April 23, 1937.

U.M.M.Z. No. 125016: 3 yearlings 58 to 64 mm. long, collected by Carl L. Hubbs and family in Beaver Creek, near its junction with Verde River, near Camp Verde, Yavapai County (T. 14 N., R. 5 E.), Arizona; September 2, 1938.

U.M.M.Z. No. 125026: 7 young and yearling fish 47 to 76 mm. in length, obtained on the same day in Verde River, just above Camp Verde, near the mouth of Beaver Creek, Yavapai County, Arizona.

This is perhaps the most clear-cut and convincing of the hybrid combinations among the Catostomidae. In the region where hybrids were secured, the only sucker species usually present are *Catostomus insignis* and *Pantosteus clarkii,* and these species commingle in the same habitats. They are

TABLE XVI

PROPORTIONATE MEASUREMENTS OF HYBRIDS BETWEEN *Catostomus commersonnii sucklii* AND *Pantosteus delphinus delphinus*, AND OF THE PARENTAL SPECIES

The measurements are expressed as thousandths of the standard length. There are given for each item the range of the measurements; the average, in parentheses; and, as a subscript, the number of specimens.

	Hot Sulphur Springs, Colorado		Grand River System, Colorado	
Size group, mm.				
*C. c. sucklii**	32–57 $(44)_{10}$	66–125 $(98)_{7}$	.... $(155)_{1}$	189–239 $(213)_{8}$
Hybrids	34–43 $(40)_{8}$	57–71 $(64)_{2}$	.... $(128)_{1}$	.... $(231)_{1}$
P. d. delphinus	37–41 $(39)_{6}$	52–73 $(60)_{7}$	87–161 $(123)_{8}$	205–272 $(237)_{4}$
Caudal peduncle, depth				
C. c. sucklii	82–97 (93)	95–108 (98)	.... (97)	88–95 (91)
Hybrids	79–85 (82)	83–90 (87)	.... (84)	.... (90)
P. d. delphinus	73–79 (76)	75–83 (78)	68–76 (73)	70–74 (72)
Head length				
C. c. sucklii	279–305 (293)	264–293 (283)	.... (272)	238–276 (255)
Hybrids	252–284 (273)	256–285 (271)	.... (275)	.... (249)
P. d. delphinus	269–284 (277)	249–260 (256)	218–246 (234)	216–227 (222)
Head depth				
C. c. sucklii	171–182 (178)	155–181 (173)	.... (164)	156–167 (163)
Hybrids	156–165 (160)	156–169 (163)	.... (163)	.... (158)
P. d. delphinus	153–159 (155)	142–155 (149)	137–154 (144)	139–148 (145)
Head width				
C. c. sucklii	163–175 (168)	155–176 (166)	.... (166)	154–171 (164)
Hybrids	149–155 (152)	152–168 (160)	.... (171)	.... (168)
P. d. delphinus	154–163 (159)	153–167 (159)	158–170 (165)	168–175 (171)
Isthmus width				
C. c. sucklii	32–53 (42)	37–52 (47)	.... (50)	41–58 (49)
Hybrids	50–62 (55)	59–72 (65)	.... (66)	.... (56)
P. d. delphinus	77–103 (84)	63–87 (78)	79–104 (92)	98–135 (118)

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* The figures entered for the *Catostomus* for Hot Sulphur Springs are transferred from Table II, which is based on material from the North Platte River of Wyoming and Nebraska, since none were secured at Hot Sulphur Springs and the species was probably introduced into the Upper Colorado River from the Platte River system.

TABLE XVI—(*Cont.*)

PROPORTIONATE MEASUREMENTS OF HYBRIDS BETWEEN *Catostomus commersonnii sucklii* AND *Pantosteus delphinus delphinus*, AND OF THE PARENTAL SPECIES

	Hot Sulphur Springs, Colorado		Grand River System, Colorado	
Snout length				
C. c. sucklii	103–125 (114)	116–136 (126)	.... (139)	126–145 (133)
Hybrids	99–110 (105)	116–132 (124)	.... (146)	.... (142)
P. d. delphinus	93–105 (101)	105–122 (113)	111–136 (123)	124–145 (130)
Mouth width				
C. c. sucklii	72–85 (77)	67–90 (77)	.... (93)	82–88 (85)
Hybrids	77–83 (79)	88–103 (95)	.... (96)	.... (93)
P. d. delphinus	88–103 (95)	100–117 (110)	96–122 (111)	98–115 (105)
Cartilaginous ridge, width				
C. c. sucklii	40–48 (42)	39–53 (45)	.... (45)	39–42 (40)
Hybrids	46–50 (48)	55–56 (55)	.... (45)	.... (49)
P. d. delphinus	58–63 (60)	57–67 (62)	62–76 (69)	65–73 (69)
Mouth length				
C. c. sucklii	51–63 (56)	52–63 (56)	.... (65)	63–70 (67)
Hybrids	60–62 (61)	65–66 (65)	.... (72)	.... (72)
P. d. delphinus	54–66 (63)	63–76 (70)	68–84 (77)	75–84 (77)
Lower lip, union				
C. c. sucklii	7–18 (11)	13–18 (15)	.... (14)	13–18 (15)
Hybrids	14–19 (17)	17–19 (18)	.... (19)	.... (15)
P. d. delphinus	21–27 (24)	25–33 (27)	33–40 (36)	28–38 (34)

TABLE XVII

RELATIVE NUMBERS OF HYBRIDS, *Catostomus insignis* × *Pantosteus clarkii*, AND OF THE PARENTAL SPECIES

Specimens in University of Michigan Museum of Zoology	*Catostomus insignis*	Hybrids	*Pantosteus clarkii*
In collection containing hybrid			
U.M.M.Z. No. 110433	32	1	18
U.M.M.Z. No. 118175	116	3	68
U.M.M.Z. No. 121642	14	6	36
U.M.M.Z. No. 121646	55	1	18
U.M.M.Z. No. 125016	96	3	168
U.M.M.Z. No. 125026	36	7	108
Total	349	21	416
From the Gila River system	1256	21	2069

strikingly different in a large number of characters, and the hybrids are consistently intermediate.

The dorsal rays average 11.00, a little less than midway between the mean of 11.32 for *C. insignis* and average of 10.59 for *P. clarkii* (Table XXXII).

The average number of the scales in this combination intervenes nicely between the means for the parental species (Tables XXXIII to XXXVII; Fig. 7). This is a particularly significant fact, in view of the very peculiar squamational pattern of *P. clarkii,* in which the scales are small except on the anterior part of the back, where they are spectacularly increased in size. In the series along the lateral line, below the lateral line, and around the caudal peduncle *clarkii* has finer scales than has *insignis;* but before the dorsal, and to a lesser degree in the row above the lateral line, the relation is reversed, in that *clarkii* here has fewer scales than does *insignis.* But in all series the hybrids are intermediate.

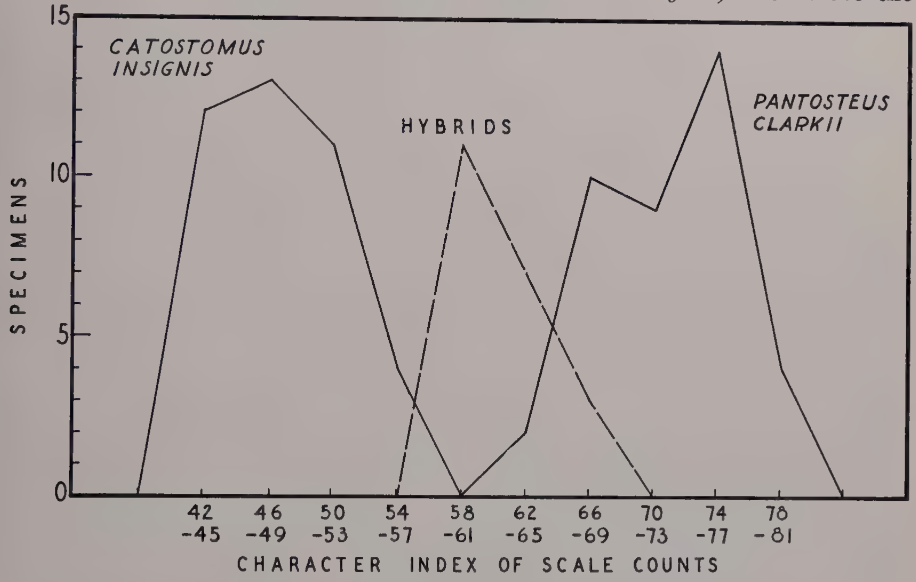

FIG. 5. Comparison of hybrids, *Catostomus insignis* × *Pantosteus clarkii,* with the parental species in the character index of scale counts (Table XVIII).

Much of the overlap between the scale counts of the hybrids and those of each parental form can be eliminated by combining all the enumerations of each specimen into a single index:

> (Scales in lateral line + scales below lateral line + scales around caudal peduncle) minus (scales before dorsal + scales above lateral line).

As shown in Table XVIII and in Figure 5 most of the indices for the hybrids are intercalated between the adjacent extremes of variation of the parental species. Thus, we again confirm the interpretation of the aberrant specimens as hybrids and verify the view that systematic characters do not mendelize in inheritance.

The hybrids display their origin and the mode of inheritance involved in almost all the proportionate measurements (Table XIX). Of the 10 measurements taken, only the head width fails to bear significantly on the problem. The length of the snout gives data that is hardly trustworthy, though the averages for the hybrids do lie between those for the parental species. Strikingly intermediate are the average values, in the hybrids, of the following proportionate measurements: depth of caudal peduncle, length and depth of head, width of isthmus, length and width of mouth, width of cartilaginous ridge of lower jaw, and length of union of lower lip.

TABLE XVIII

FREQUENCY DISTRIBUTION OF THE CHARACTER INDEX FOR SCALE COUNTS IN HYBRIDS, *Catostomus insignis* × *Pantosteus clarkii*, AND IN THE PARENTAL SPECIES

The index is derived by summing the counts of scales along lateral line, below lateral line, and around caudal peduncle; then subtracting from this sum the count of scales above the lateral line plus the predorsal scale count.

	Character Index for Scale Count									
	42–45	46–49	50–53	54–57	58–61	62–65	66–69	70–73	74–77	78–81
Catostomus insignis	12	13	11	4	......	......	......	......	......	......
Hybrids	......	......	......	......	11	7	3	......	......	......
Pantosteus clarkii	......	......	......	......	......	2	10	9	14	4

	Statistical Computations					
	No.	Range	Ave.*	S.E.*	V	Hybrid index $\pm$ S.E.$_{\mathrm{I}}$
Catostomus insignis	40	42–55	48	.61	8.0	....
Hybrids	21	58–68	62	.69	5.1	58 ± 12
Pantosteus clarkii	39	65–81	72	.66	5.7	....

* Computed from the original, unclassed data.

In this combination the origin of the hybrids is particularly well shown by the structure of the mouth. The difference between the parental species involves all of the features mentioned in discussing the intergeneric hybrids (pp. 33–36). A very striking contrast is offered because the mouth of *P. clarkii* is especially extreme (Pl. I, Fig. 3*c*): it is extremely broad, and the gape almost strictly transverse; the lower lip is very full, and the median incision is shallow; the lateral emarginations are very deep. The mouths of the hybrids are invariably intermediate in structure (Pl. I, Figs. 3*a–c*) and obliquity (Pl. VI, Figs. 3*a–c*), and are almost always of intervening values in the dimensions (Fig. 4). Some specific features of *C. insignis*, such as the extreme turgidity of both lips and the fine, thick-set papillary pattern, are well reflected in the hybrids.

The character index for mouth and isthmus dimensions (Fig. 4) not only has intermediate values in the hybrids, but also indicates an intermediate relative growth for these dimensions. The index falls with age in *Catosto-*

TABLE XIX

PROPORTIONATE MEASUREMENTS OF HYBRIDS BETWEEN *Catostomus insignis* AND *Pantosteus clarkii*, AND OF THE PARENTAL SPECIES

The measurements are expressed as thousandths of the standard length. There are given for each item the range of the measurements; the average, in parentheses; and, as a subscript, the number of specimens.

	Verde River, Arizona	East Branch, Black River, Arizona		Taylor Creek, New Mexico	
Size group, mm.					
C. insignis	51–84 (63)$_{15}$	77–90 (84)$_{6}$	91–118 (104)$_{8}$	48–57 (52)$_{4}$	93–167 (134)$_{6}$
Hybrids	47–76 (59)$_{10}$	73–84 (78)$_{5}$	94–102 (98)$_{2}$	51–57 (54)$_{2}$	110–138 (124)$_{2}$
P. clarkii	49–92 (61)$_{15}$	58–78 (64)$_{9}$	91–179 (125)$_{6}$	49–82 (62)$_{6}$	127–163 (146)$_{4}$
Caudal peduncle, depth					
C. insignis	85–101 (94)	105–113 (109)	100–115 (107)	100–106 (103)	99–107 (102)
Hybrids	82–96 (88)	94–102 (98)	100–100 (100)	90–96 (93)	94–97 (95)
P. clarkii	76–87 (82)	93–103 (97)	83–98 (93)	78–88 (85)	80–90 (84)
Head length					
C. insignis	273–297 (284)	265–289 (278)	261–276 (271)	287–315 (302)	257–282 (267)
Hybrids	261–281 (273)	260–272 (267)	260–261 (261)	284–291 (277)	254–279 (267)
P. clarkii	245–272 (255)	255–281 (268)	224–267 (248)	237–274 (258)	232–257 (244)
Head depth					
C. insignis	172–193 (183)	186–195 (188)	172–190 (181)	189–204 (197)	170–188 (179)
Hybrids	165–180 (175)	172–180 (178)	164–176 (170)	184–185 (185)	162–172 (167)
P. clarkii	153–171 (163)	166–181 (173)	137–182 (161)	150–165 (160)	143–157 (151)
Head width					
C. insignis	162–191 (176)	158–192 (180)	166–187 (176)	185–191 (187)	168–182 (176)
Hybrids	162–176 (171)	179–185 (182)	168–183 (177)	176–186 (181)	173–179 (176)
P. clarkii	161–176 (169)	183–196 (187)	178–190 (184)	166–174 (170)	168–197 (182)
Isthmus width					
C. insignis	63–81 (70)	50–69 (61)	57–71 (63)	67–78 (70)	56–66 (64)
Hybrids	75–95 (84)	74–82 (78)	78–81 (79)	78–92 (85)	74–78 (76)
P. clarkii	93–115 (109)	104–121 (112)	99–111 (105)	101–120 (111)	94–113 (106)

TABLE XIX—(*Cont.*)

PROPORTIONATE MEASUREMENTS OF HYBRIDS BETWEEN *Catostomus insignis* AND *Pantosteus clarkii*, AND OF THE PARENTAL SPECIES

The measurements are expressed as thousandths of the standard length. There are given for each item the range of the measurements; the average, in parentheses; and, as a subscript, the number of specimens.

	Verde River, Arizona	East Branch, Black River, Arizona		Taylor Creek, New Mexico	
Snout length					
C. insignis	116–136 (129)	121–150 (141)	119–140 (133)	128–143 (136)	132–145 (138)
Hybrids	109–142 (121)	128–142 (134)	126–135 (131)	128–139 (133)	133–142 (137)
P. clarkii	108–135 (118)	125–141 (133)	120–135 (129)	122–138 (127)	127–145 (135)
Mouth width					
C. insignis	71–96 (81)	85–99 (93)	78–104 (89)	89–108 (97)	78–96 (85)
Hybrids	78–117 (92)	111–125 (117)	105–113 (109)	108–119 (113)	111–114 (113)
P. clarkii	90–126 (110)	125–137 (132)	127–152 (137)	116–137 (124)	120–143 (130)
Cartilaginous ridge, width					
C. insignis	38–52 (44)	37–43 (39)	31–41 (34)	37–51 (41)	29–41 (37)
Hybrids	48–67 (53)	44–53 (50)	50–56 (53)	55–55 (55)	55–55 (55)
P. clarkii	58–76 (67)	66–76 (70)	68–77 (71)	63–67 (66)	66–70 (68)
Mouth length					
C. insignis	53–76 (60)	49–72 (57)	50–72 (62)	67–73 (71)	66–82 (75)
Hybrids	52–87 (67)	76–89 (84)	74–83 (79)	85–87 (86)	85–86 (85)
P. clarkii	57–89 (71)	80–95 (88)	83–97 (91)	80–94 (87)	84–93 (87)
Lower lip, union					
C. insignis	9–14 (12)	12–20 (16)	12–19 (15)	9–20 (13)	12–18 (15)
Hybrids	12–24 (18)	21–27 (23)	25–27 (26)	19–27 (23)	25–29 (27)
P. clarkii	29–39 (35)	33–42 (36)	37–50 (43)	37–42 (39)	42–46 (43)

mus insignis, rises in *Pantosteus clarkii,* and remains about even in the hybrids.

As usual the hybrids are also intermediate in form of snout, in coloration, and in other characters (Pl. VI, Fig. 3). They tend to show their specific relationship to *C. insignis* in the development of dark spots on the scale pockets.

The intermediacy of the hybrids is beautifully shown by the limited deviation of the hybrid indices from the mean percentage value of 50 (Table

XXXIX). The total range is 25 to 67, and in 17 of the 21 hybrids the indices vary from 39 to 63.

7. *Catostomus,* species × *Pantosteus santa-anae*

(Fig. 6; Pl. I, Fig. 1*b*; Pl. VII, Fig. 1*b*)

U.M.M.Z. No. 131653: 1 young or yearling 45 mm. in standard length, seined by Robert R. and Ralph G. Miller in Santa Clara River 4.6 miles by road east of Piru, Ventura County, California; July 9, 1940.

U.M.M.Z. No. 131666: 5 adults 99 to 114 mm. long, taken by the same collectors in Sespe Creek, a tributary of Santa Clara River, 4.5 miles north-northwest of Fillmore, Ventura County, California; same date.

U.M.M.Z. No. 140484: 38 subadults and adults, 87–184 mm. long, secured by the same collectors in Sespe Creek, at base of dam about 0.5 mile above point where the collection was made in 1940; October 2, 1942.

TABLE XX

RELATIVE NUMBERS OF HYBRIDS, *Catostomus,* SPECIES × *Pantosteus santa-anae,* AND OF THE PARENTAL SPECIES

Specimens in University of Michigan Museum of Zoology	*Catostomus,* species	Hybrids	*Pantosteus santa-anae*
In collection containing hybrid			
U.M.M.Z. No. 131653	0	1	385
U.M.M.Z. No. 131666	2	5	207
U.M.M.Z. No. 140484	2	38	229
Total	4	44	825
From the Santa Clara System			
1934	......	......	355
1939	1	......	349
1940	2	6	845
1941	......	......	125
1942	2	38	234
Total	5	44	1907

The information on the collection of these hybrids and of the parental species poses a difficult problem. No species of sucker has been reported from the Santa Clara River system, though we have known for some years that this drainage is inhabited by *Pantosteus santa-anae* Snyder (1908)—the only species of the family hitherto known from the coastal streams of Southern California. Obviously one parent is this *Pantosteus,* which is locally abundant in the region where the hybrids were secured. The other parental species is obviously referable to *Catostomus,* but in the confused status of the taxonomy of this genus in the West Coast drainage it is inadvisable to attempt at present a more specific determination.

Since in 1939 a single specimen of this *Catostomus* was seined in Santa Clara River, a return trip was made to the region in 1940. Vigorous collecting in nearly all available habitats yielded only 2 more specimens (in Sespe Creek), along with hundreds of the *Pantosteus* and the 6 hybrids (1 from Santa Clara River; 5 from Sespe Creek).

In 1942 Sespe Creek was again visited. The seining was done in deep pools below a dam, for it was thought that the *Catostomus* might favor such a habitat. Only 2 specimens of this genus were obtained, however, along with the impressive number of 38 hybrids and 229 mountain suckers (*Pantosteus*). Of the *Pantosteus* 119 were discarded in the field after having been carefully checked by Robert R. Miller to make sure that no *Catostomus* and no hybrid was included. We are deeply grateful to Miller for his cooperation in this study. He obtained all of the hybrids of this combination.

Two explanations for the rarity of *Catostomus* in the Santa Clara River system offer themselves:

(1) It is a native species which was formerly common in the deeper holes but which is now approaching extinction because the surface waters are being consumed in irrigation and perhaps also because the holes in the river are being filled with flood washings. In years of more ample and more regular water supply this species and the *Pantosteus* may well have had a complementary distribution in the stream system; now they are forced to live together.

TABLE XXI

SEX RATIOS OF HYBRIDS BETWEEN *Catostomus*, SPECIES AND *Pantosteus santa-anae*, AND OF THE PARENTAL SPECIES

	Catostomus, species		Hybrids		*Pantosteus santa-anae*	
	Males	Females	Males	Females	Males	Females
Numbers	3	2	17	27	51	59*
Percentages	?	?	39	61	46	54*

* The slight preponderance of females in the *Pantosteus* sample, collected in 1942, may be explained by the facts that many of the suckers were discarded in the field, and that the largest ones, predominantly females, were preserved.

(2) It is an introduced species which has not become well established and which, like *Catostomus commersonnii sucklii* in the Colorado system (pp. 12–13 and 39), has been thrown out of adjustment with its environment. This alternative seems the less plausible, but is not readily to be excluded because we find very little basis, if any, for distinguishing the specimens taken in the Santa Clara from those collected in certain other watersheds in California.

Either theory offers conditions which, to judge from our studies on the hybridization of fish species in nature, would be conducive to the intermating of species and to the local extirpation of the rare parental form. The number of species of each category collected each year (Table XX) provides a slight indication that the population of the *Catostomus* has been encountered in the last stages of its decimation. It certainly seems probable that the number of hybrids has been increasing. In this connection it is of interest to note that the gonads of the hybrids and of the *Catostomus* specimens collected on October 2, 1942, showed evidence of little to no spawning during the previous breeding season. Most of the testes were large, and most of the ovaries were turgid with medium-sized eggs, not flabby and with relatively few eggs as in the *Pantosteus* specimens. The sex-ratio may be slightly altered in the hybrids (Table XXI).

The average values for the counts (Tables XXXII to XXXVII) are unusually close in the Santa Clara River forms of *Catostomus* and *Pantosteus* and hence offer a poorer test than usual of the behavior of characters in species crosses. A small difference between the species, with the hybrids intermediate on the average, is indicated by the counts of dorsal rays and of scales in the lateral line, in the predorsal region, and around the caudal peduncle. The number of scales in the transverse series (above and below the lateral line), however, averages a little higher in the hybrids than in either parental species. This unusual relation may represent a true condition. The greater number of scales in the transverse series may well be correlated with the greater depth of the body in the hybrids (Table XXII). In the minnow hybrid, *Gila orcuttii* × *Siphateles mohavensis*, a similar increase in transverse scale counts and in depth of body has been demonstrated and regarded as probably due to heterosis (Hubbs and Miller, 1943). The head averages longer than in either parental species, and the head and the caudal peduncle average about as deep and the dorsal fin about as large as in the *Catostomus;* the *Gila* × *Siphateles* hybrid is also large-headed and big-finned. In the head width, probably in the snout length, and certainly in the isthmus width and in all of the mouth measurements (which are particularly significant), the hybrids are intermediate between the *Catostomus* and the *Pantosteus* (some of these proportions are higher for the 1942 collections than for those of 1939 and 1940, due to the better preservation of the specimens). The interjacence of the hybrids is especially well shown by the character index which expresses the mouth and isthmus measurements (Table XI). The mouths of the hybrids show not only the usual features of intermediacy displayed by any of the *Catostomus* × *Pantosteus* crosses (pp. 33–36), but also present in diluted form the special peculiarities of each of the local parental species (Pl. I, Figs. 1*a–c;* Pl. VII, Figs. 1*a–c*).

The hybrid indices when summarized for individuals (Table XXXIX) fluctuate over a rather wide range, but tend toward an interjacent position. The mean value (41) is the lowest for any of the hybrid combinations. The variability and the low value are both caused by the peculiar relationships discussed in the preceding paragraph.

The intermediate hybrid nature of the aberrant suckers from the Santa Clara River system was confirmed by an analysis of an osteological character (Fig. 6), as represented in the 5 large specimens collected prior to 1942. The *Catostomus* species involved has a well-developed suboblong parietal fontanelle in the cranium, *Pantosteus santa-anae* typically has the fontanelle closed in the half-grown and adult, and the hybrids have an opening of

TABLE XXII

PROPORTIONATE MEASUREMENTS OF HYBRIDS BETWEEN *Catostomus*, SPECIES AND *Pantosteus santa-anae*, AND OF THE PARENTAL SPECIES

The measurements are expressed as thousandths of the standard length. There are given for each item the range of the measurements; the average, in parentheses; and, as a subscript, the number of specimens.

	Sespe Creek, 1942		Santa Clara River and Sespe Creek, 1939–40	Santa Clara River, 1940
Measured by	Hubbs		Johnson	Johnson
Size group, mm.				
Catostomus, sp.	....	92–109 $(101)_2$	120–153 $(142)_3$	....
Hybrids	141–184 $(167)_5$	87–130 $(109)_{38}$	99–114 $(108)_5$	.... $(45)_1$
P. santa-anae	....	93–123 $(102)_9$	89–126 $(108)_{22}$	39–49 $(42)_{15}$
Body depth				
Catostomus, sp.	....	227–251 (239)	204–252 (222)	....
Hybrids	224–239 (232)	223–268 (243)	219–233 (226)	.... (188)
P. santa-anae	....	214–238 (226)	173–263 (197)	188–214 (201)
Caudal peduncle, depth				
Catostomus, sp.	....	93–104 (99)	86–98 (92)	....
Hybrids	97–101 (99)	91–104 (98)	96–98 (97)	.... (97)
P. santa-anae	....	86–97 (90)	78–92 (85)	89–98 (93)
Head length				
Catostomus, sp.	....	243–268 (255)	226–247 (236)	....
Hybrids	256–265 (263)	247–277 (264)	251–263 (256)	.... (272)
P. santa-anae	....	254–269 (263)	231–264 (249)	266–286 (278)
Head depth				
Catostomus, sp.	....	163–174 (169)	144–152 (149)	....
Hybrids	162–173 (168)	154–184 (169)	158–170 (162)	.... (160)
P. santa-anae	....	155–171 (164)	136–159 (149)	161–170 (166)
Head width				
Catostomus, sp.	....	161–172 (167)	148–159 (153)	....
Hybrids	172–190 (181)	168–187 (177)	158–163 (161)	.... (156)
P. santa-anae	....	175–188 (182)	152–175 (161)	153–170 (164)

TABLE XXII—(*Cont.*)

	Sespe Creek, 1942		Santa Clara River and Sespe Creek, 1939–40	Santa Clara River, 1940
Measured by	Hubbs		Johnson	Johnson
Snout length				
Catostomus, sp.	....	112–113 (113)	107–120 (113)	....
Hybrids	120–131 (127)	109–130 (122)	113–134 (126)	.... (125)
P. santa-anae	....	123–139 (132)	105–132 (118)	107–126 (117)
Mouth width				
Catostomus, sp.	....	79–82 (81)	78–82 (80)	....
Hybrids	90–101 (94)	89–110 (99)	95–104 (99)	.... (104)
P. santa-anae	....	119–134 (127)	94–117 (107)	111–126 (117)
Cartilaginous ridge, width				
Catostomus, sp.	....	39–44 (41)	35–43 (39)	....
Hybrids	48–54 (51)	44–56 (51)	42–51 (47)	.... (47)
P. santa-anae	....	59–68 (64)	47–61 (54)	52–62 (57)
Mouth length				
Catostomus, sp.	....	51–54 (53)	49–57 (54)	....
Hybrids	60–71 (64)	59–79 (69)	62–72 (69)	.... (71)
P. santa-anae	....	84–95 (90)	66–80 (73)	71–85 (79)
Lower lip, union				
Catostomus, sp.	....	15–22 (19)	14–17 (15)	....
Hybrids	21–29 (25)	20–29 (25)	15–22 (19)	.... (19)
P. santa-anae	....	37–48 (42)	28–40 (35)	28–37 (33)
Isthmus width				
Catostomus, sp.	....	.... (64)*	33–55 (45)	....
Hybrids	79–87 (81)	63–94 (81)	56–74 (66)	.... (64)
P. santa-anae	....	83–116 (98)	56–98 (78)	57–91 (80)

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* In the smaller of the two hybrids in this set the gill membranes form a free fold across the isthmus, as in the teratological suckers described by Hubbs (1914*a*). In this specimen the scales are not increased in number as they were in the terata previously described; on the contrary the lateral line count is extremely low (69). The isthmus measurement of this aberrant fish is not included.

TABLE XXII—(*Cont.*)

Proportionate Measurements of Hybrids between *Catostomus*, Species and *Pantosteus santa-anae*, and of the Parental Species

	Sespe Creek, 1942		Santa Clara River and Sespe Creek, 1939–40	Santa Clara River, 1940
Measured by	Hubbs		Johnson	Johnson
Dorsal fin to occiput, distance				
Catostomus, sp.	....	285–288 (287)	256–274 (266)	....
Hybrids	281–300 (292)	274–301 (288)	240–261 (252)	.... (267)
P. santa-anae	....	269–298 (285)	242–284 (270)	239–263 (252)
Dorsal fin base				
Catostomus, sp.	....	154–182 (168)	153–180 (168)	....
Hybrids	171–188 (183)	157–188 (172)	162–179 (167)	.... (180)
P. santa-anae	....	147–196 (167)	133–164 (147)	142–160 (151)
Depressed dorsal fin, length				
Catostomus, sp.	....	233–301 (267)	233–292 (268)	....
Hybrids	254–280 (267)	241–300 (267)	253–283 (268)	.... (271)
P. santa-anae	....	233–286 (255)	207–254 (225)	235–255 (247)

TABLE XXIII

Dimensions of the Parietal Fontanelle in Hybrids between *Catostomus*, Species and *Pantosteus santa-anae*, and in the Parental Species

	Standard length, mm. (L)	Length of Fontanelle	Width of Fontanelle	Area, mm² (A)	Relative Area $\left(\frac{100\sqrt{A}}{L}\right)$
Catostomus, species	119	6.51	1.70	9.48	2.59
	152	8.30	1.49	9.99	2.08
	153	7.80	1.90	11.70	1.90
Hybrids	99	5.16	0.89	3.47	1.88
	108	4.85	1.20	2.85	1.56
	109	5.86	0.97	3.53	1.72
	110	5.32	1.00	3.70	1.75
	114	5.39	1.23	3.35	1.61
Pantosteus santa-anae	99	3.12	0.20	0.35	0.60
	107	1.90	0.19	0.25	0.00
	109.5	0.00	0.00	0.00	0.49
	114	0.00	0.00	0.00	0.00
	115	0.00	0.00	0.00	0.00
	117.5	0.00	0.00	0.00	0.00
	126	0.00	0.00	0.00	0.00
Average					
Catostomus, species	141	7.54	1.70	10.39	2.30
Hybrids	108	5.32	1.06	3.38	1.70
Pantosteus	113	0.72	0.06	0.08	0.15

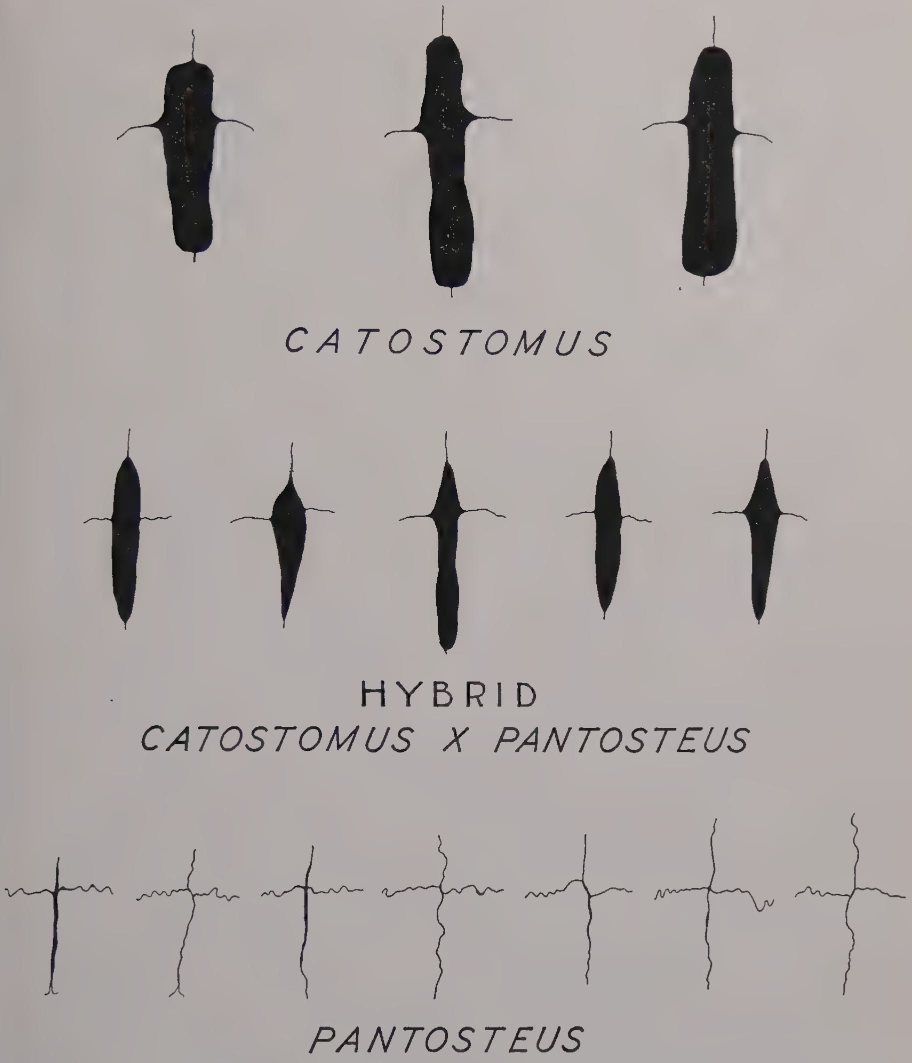

Fig. 6. Comparison of parietal fontanelles in hybrids, *Catostomus*, species × *Pantosteus santa-anae*, and in the parental species (Table XXIII).

All figures were drawn to the same scale with the aid of a camera lucida.

Top row, *Catostomus*, species: left, from specimen 120 mm. long, taken in Santa Clara River, Ventura County, California; center and right, from specimens respectively 152 and 153 mm. long, seined with the hybrids.

Middle row, hybrids: from right to left, drawn from 5 specimens grading from 99 to 114 mm. in length (U.M.M.Z. No. 131666).

Bottom row, *Pantosteus santa-anae:* sketched from 7 specimens, grading from 99 mm. (at left) to 126 mm. long.

intermediate size. The fontanelle in the hybrids tends to be pointed fore and aft. The length and width figures as well as the area computations are given in Table XXIII. The area was obtained by proportion from (1) the length of the fontanelle as measured on the specimen to .01 mm., with precision dial calipers; (2) the length of the opening as measured on the figure, which was carefully drawn with the aid of a camera lucida; (3) the area of the sketch of the fontanelle, determined by planimeter. The hybrid indices average 33 for the length, 39 for the width, and 28 for the relative area of the fontanelle. The closer approach toward the *Catostomus* thus indicated may be due to the facts that the fontanelle tends to become reduced in relative size with age, and that the measured hybrids average smaller than the 3 specimens of the *Catostomus* which were examined for this character.

8. *Catostomus tahoensis* × *Pantosteus lahontan*

(Pl. I, Fig. 2*b*; Pl. VII, Fig. 2*b*)

U.M.M.Z. No. 124861: 3 half-grown measuring 71 to 84 mm. in standard length, collected by Carl L. Hubbs and family in Carson River, 2 miles west of Fallon, Nevada, at an elevation of 3970 feet; July 30, 1938.

U.M.M.Z. No. 124870: 1 half-grown 96 mm. long, obtained on the same expedition in Humboldt River at Irish-American Dam, about 3 miles northeast of Lovelock, Nevada; July 31, 1938.

U.M.M.Z. No. 124919: 3 young to small adult fish 35.5 to 128 mm. long, also taken on the same trip, in Hot Creek, tributary to Pony Creek and thence to Pine Creek, in the Humboldt River system in Eureka County, 31.6 miles by road south of Carlin, Nevada; August 12, 1938.

U.M.M.Z. No. 133688: a breeding pair 106 and 122 mm. long, collected by Garth Murphy in Little Truckee River just above the head of Boca Dam, about 7 miles east of Truckee, Nevada County, California; June 26, 1940.

U.M.M.Z. No. 133816: 1 half-grown 86 mm. in length, taken by J. R. Alcorn in Carson River at Coleman Dam, Churchill County, Nevada; April 27, 1940.

U.M.M.Z. No. 136273: 1 yearling 46 mm. long, seined by Carl L. Hubbs and family in North Fork of Humboldt River near mouth, Elko County, Nevada, June 29, 1942.

U.M.M.Z. No. 136274: 1 adult of 123.5 mm., taken on the same trip in Truckee River, 3.3 miles above Wadsworth, Washoe County, Nevada, July 22, 1942.

U.M.M.Z. No. 140235: 6 yearling to small adult specimens 67–118 mm. long, seined by Robert R. Miller and party in Little Truckee River, 14 miles north of Truckee, Sierra County, California; August 15, 1942.

U.M.M.Z. No. 140243: 2 yearlings 44 to 55 mm. long, taken on the same expedition in Prosser Creek, 4.5 miles north of Truckee, Nevada County, California; August 15, 1942.

U.M.M.Z. No. 140285: 3 young and 1 small adult 24 to 96 mm. long, secured on the same trip in a distributary of the East Fork of Carson River, Douglas County, Nevada; August 19, 1942.

U.M.M.Z. No. 140302: 2 adults 157 to 165 mm. long, obtained by the same party in Carson River, 12 miles east of Carson City, Nevada; August 20, 1942.

U.M.M.Z. No. 140370: 1 half-grown of 80 mm., seined on the same trip in a distributary of Buckeye Creek, about 3 miles north of Bridgeport, Mono County, California; August 26, 1942.

U.M.M.Z. No. 140390: a 68 mm. yearling, also taken on the same expedition in a distributary of Buckeye Creek, below Highway 395; August 28, 1942.

These hybrids between the 2 common suckers of the Lahontan interior drainage basin conform to the general pattern. They exhibit intermediacy in the various ways that all *Catostomus* × *Pantosteus* do (pp. 33–36).

In number of dorsal rays (Table XXXII) the hybrids yield an intermediate average despite the fact that the means for the parental species differ by only 0.28 of a ray. Though the parental differences in the scale counts are not large, intermediacy of the averages is indicated for the 10 specimens collected prior to 1942. Except for fin-ray counts no enumerations or measurements were taken on the 18 obvious hybrids collected in 1942, when the manuscript was in press.

TABLE XXIV

RELATIVE NUMBERS OF HYBRIDS, *Catostomus tahoensis* × *Pantosteus lahontan*, AND OF THE PARENTAL SPECIES

Specimens in University of Michigan Museum of Zoology	*Catostomus tahoensis*	Hybrids	*Pantosteus lahontan*
In collection containing hybrid			
U.M.M.Z. No. 124861	88	3	39
U.M.M.Z. No. 124870	13	1	177
U.M.M.Z. No. 124919	7	3	70
U.M.M.Z. No. 133688	2	2	16
U.M.M.Z. No. 133816	1	1	1
U.M.M.Z. No. 136273	12	1	46
U.M.M.Z. No. 136274	85	1	5
U.M.M.Z. No. 140235	33	6	31
U.M.M.Z. No. 140243	10	2	49
U.M.M.Z. No. 140285	50	4	181
U.M.M.Z. No. 140302	58	2	57
U.M.M.Z. No. 140370	80	1	4
U.M.M.Z. No. 140390	51	1	1
Total	500	28	677
From the Lahontan system	3282*	28	2007

* Perhaps one-third of the *Catostomus* specimens were collected in places where neither the *Pantosteus* nor hybrids occur. *Pantosteus* is very generally accompanied by *Catostomus*.

In either 2 or all 3 of the series as tabulated, representing either 9 or 10 of the 10 specimens, the average values for the following proportionate measurements of the hybrids measured (Table XXV) intervene between those of the parental species: length, depth, and width of the head, the width of the isthmus, and all the mouth measurements. The length of the snout shows nothing important, and there is some doubt as to the significance of the head-width proportion. The form of the snout, as well as that of the mouth, however, bespeaks the origin of the hybrid (Pl. I, Figs. 2*a*–*c*; Pl. VII, Figs. 2*a*–*c*).

The 10 individual hybrid indices based on all counts and measurements vary from 15 to 86, and average 44, not far below the theoretically perfect intermedial value of 50 (Table XXXIX).

TABLE XXV

PROPORTIONATE MEASUREMENTS OF HYBRIDS BETWEEN *Catostomus tahoensis* AND *Pantosteus lahontan*, AND OF THE PARENTAL SPECIES

The measurements are expressed as thousandths of the standard length. There are given for each item the range of the measurements; the average, in parentheses; and, as a subscript, the number of specimens.

	Carson and Humboldt Rivers and Hot Creek, Nevada		Little Truckee River, California
Size group, mm.			
C. tahoensis	32–43 $(37)_8$	62–89 $(76)_{12}$	77–134 $(105)_2$
Hybrids	…… $(35)_1$	71–128 $(89)_7$	106–122 $(114)_2$
P. lahontan	31–53 $(35)_{10}$	63–99 $(80)_{20}$	87–108 $(97)_6$
Caudal peduncle, depth			
C. tahoensis	75–84 (79)	86–95 (89)	90–95 (93)
Hybrids	…… (86)	83–96 (88)	95–96 (96)
P. lahontan	75–86 (81)	72–92 (84)	86–92 (90)
Head length			
C. tahoensis	260–294 (275)	246–275 (257)	248–261 (255)
Hybrids	…… (283)	241–255 (246)	242–242 (242)
P. lahontan	240–279 (264)	217–245 (233)	226–239 (235)
Head depth			
C. tahoensis	164–183 (171)	147–164 (157)	152–158 (155)
Hybrids	…… (160)	136–151 (147)	150–151 (151)
P. lahontan	141–158 (152)	122–142 (136)	129–142 (137)
Head width			
C. tahoensis	156–165 (160)	146–167 (154)	150–153 (151)
Hybrids	…… (152)	148–164 (152)	150–158 (154)
P. lahontan	147–155 (150)	137–156 (149)	149–169 (158)
Isthmus width			
C. tahoensis	52–66 (59)	57–71 (63)	52–62 (57)
Hybrids	…… (89)	68–85 (73)	75–75 (75)
P. lahontan	77–103 (89)	86–103 (94)	83–99 (91)

TABLE XXV—(*Cont.*)

PROPORTIONATE MEASUREMENTS OF HYBRIDS BETWEEN *Catostomus tahoensis* AND *Pantosteus lahontan*, AND OF THE PARENTAL SPECIES

The measurements are expressed as thousandths of the standard length. There are given for each item the range of the measurements; the average, in parentheses; and, as a subscript, the number of specimens.

	Carson and Humboldt Rivers and Hot Creek, Nevada		Little Truckee River, California
Snout length			
C. tahoensis	89–109 (97)	98–130 (111)	116–117 (117)
Hybrids	…… (102)	104–123 (112)	115–121 (118)
P. lahontan	93–110 (104)	102–117 (110)	109–129 (122)
Mouth width			
C. tahoensis	70–87 (78)	73–94 (78)	79–81 (80)
Hybrids	…… (87)	79–100 (89)	89–89 (89)
P. lahontan	74–99 (91)	91–114 (102)	93–126 (116)
Cartilaginous ridge, width			
C. tahoensis	32–47 (39)	38–46 (41)	36–39 (37)
Hybrids	…… (48)	45–50 (48)	46–49 (47)
P. lahontan	43–59 (55)	51–61 (57)	61–72 (68)
Mouth length			
C. tahoensis	44–61 (52)	46–64 (52)	53–55 (54)
Hybrids	…… (59)	57–72 (63)	60–62 (61)
P. lahontan	55–74 (65)	63–75 (69)	70–91 (80)
Lower lip, union			
C. tahoensis	9–15 (12)	10–13 (12)	13–14 (13)
Hybrids	…… (17)	20–25 (22)	20–24 (22)
P. lahontan	19–36 (25)	27–41 (35)	37–46 (41)

After the foregoing account had been prepared it was discovered that *Catostomus tahoensis* and *Pantosteus lahontan* differ in the usual number of pelvic rays, and that in this character the hybrids are almost exactly intermediate (Table XXVI).

Intermediacy of the hybrids in developmental features of pigmentation was observed in studying the 1942 collections. As the scales become developed anteriorly the scale pockets become rather sharply outlined with dark in *Pantosteus lahontan*, but are only obscurely bordered in *Catostomus tahoensis*. At this stage the pigment on the side of the head barely extends to the line passing through the lower border of the eye in the *Pantosteus,* but tends to pass below that point in the *Catostomus.* As development proceeds the lower border of the lateral band on the head is gradually extended below the eye in the *Pantosteus,* but at comparable stages the pigment extends farther down in the *Catostomus.* Furthermore, the lower margin of the pigment tends to form an even and regular line in the *Pantosteus,* so that the head appears sharply bicolored, whereas in the *Catostomus* the lower border of the pigment is less even and the lower side of the face tends to be mottled (Pl. VII, Figs. 2*a*–*c*). In all these respects the hybrids are intermediate.

TABLE XXVI

NUMBER OF PELVIC RAYS IN HYBRIDS BETWEEN *Catostomus tahoensis* AND *Pantosteus lahontan,* AND IN THE PARENTAL SPECIES*

	Number of Rays in Both Pelvic Fins								
	16	17	18	19	20	21	22	23	24
C. tahoensis	......	......	6	30	269	63	77	1	1
Hybrids	......	......	9	5	13	1	......	......	......
P. lahontan	12	17	297	24	29	......	......	......	......

	Statistical computations					
	No.	Range	Ave.	S.E.	V	Hybrid Index ± S.E.$_I$
C. tahoensis	447	18–24	20.41	.04	4.5	....
Hybrids	28	18–21	19.21	.18	4.9	52 ± 9
P. lahontan	379	16–20	18.11	.04	4.0	....

* These data were obtained too late to be used in the subsequent computations of hybrid intermediacy.

9. *Catostomus catostomus griseus* × *Pantosteus jordani*

(Pl. VII, Fig. 3*b*)

U.M.M.Z. No. 127541: 1 half-grown 98 mm. in the standard length measurement, collected by Carl L. and Laura C. Hubbs in Sweetwater River at Hudson's Ranch, Fremont County (Town 30 N., Range 95 W.), Wyoming; July 11, 1934.

TABLE XXVII

RELATIVE NUMBERS OF HYBRIDS, *Catostomus catostomus griseus* × *Pantosteus jordani,* AND OF THE PARENTAL SPECIES

Specimens in University of Michigan Museum of Zoology	*Catostomus catostomus griseus*	Hybrids	*Pantosteus jordani*
In collection containing hybrid			
U.M.M.Z. No. 127541	2	1	55
U.M.M.Z. No. 127548	13	1	1
Total	15	2	56
From the Platte River system	692*	2	81

* Some of these specimens came from localities below the known altitudinal range of *Pantosteus jordani.*

TABLE XXVIII

PROPORTIONATE MEASUREMENTS OF HYBRIDS BETWEEN *Catostomus catostomus griseus* AND *Pantosteus jordani*, AND OF THE PARENTAL SPECIES

The measurements are expressed as thousandths of the standard length. There are given for each item the range of the measurements; the average, in parentheses; and, as a subscript, the number of specimens.

Sweetwater River and Alkali Creek, Wyoming			
Size group, mm.		Snout length	
C. c. griseus	79–173 (118)$_{12}$	*C. c. griseus*	105–135 (117)
Hybrid	……… (98)$_{1}$	Hybrid	……… (115)
P. jordani	83–125 (98)$_{10}$	*P. jordani*	105–112 (109)
Caudal peduncle, depth		Mouth width	
C. c. griseus	79–95 (86)	*C. c. griseus*	84–93 (88)
Hybrid	……… (93)	Hybrid	……… (93)
P. jordani	81–88 (85)	*P. jordani*	94–110 (102)
Head length		Cartilaginous ridge, width	
C. c. griseus	241–266 (258)	*C. c. griseus*	43–48 (46)
Hybrid	……… (235)	Hybrid	……… (52)
P. jordani	210–232 (220)	*P. jordani*	61–70 (66)
Head depth		Mouth length	
C. c. griseus	138–153 (148)	*C. c. griseus*	59–70 (66)
Hybrid	……… (136)	Hybrid	……… (64)
P. jordani	122–138 (129)	*P. jordani*	60–72 (66)
Head width		Lower lip, union	
C. c. griseus	155–171 (161)	*C. c. griseus*	10–17 (13)
Hybrid	……… (152)	Hybrid	……… (27)
P. jordani	143–150 (147)	*P. jordani*	30–41 (37)
Isthus width			
C. c. griseus	60–71 (64)		
Hybrid	……… (73)		
P. jordani	85–102 (92)		

U.M.M.Z. No. 127548: 1 yearling seined by Carl L. Hubbs and family in Alkali Creek, a tributary of Sweetwater River, 14 miles by road from U. S. Highway 87W toward the Red Desert, Fremont County (T. 29 N., R. 96 W.), Wyoming; July 11, 1934.

Since hybrid No. 127548 became misplaced before detailed counts and measurements were taken, nothing more can be said of it than that it was compared with No. 127541 and found similar, that it was also intermediate between the assigned parental species, and that an identification of the hybrid as between *Catostomus commersonnii sucklii* and *Pantosteus jordani* seemed excluded by such characters as a high scale count. *C. c. sucklii* was collected with the hybrids (44 with No. 127541 and 24 with No. 127548).

There can be no doubt that 1 parent of these 2 hybrids was *Pantosteus jordani* (if that is the proper name for the form occupying Sweetwater River). That the other parent was *C. catostomus griseus* rather than *C. commersonii sucklii* seems evident from the high scale counts (Tables XXXIII–XXXVII; Fig. 7). No. 127541 shows scale counts that intervene nicely between the means for *griseus* and *jordani.* The dorsal ray count (Table XXXII) is inconclusive.

In its proportionate measurements (Table XXVIII) the single hybrid at hand is intermediate between *griseus* and *jordani* in the length, depth, and width of the head, the width of the isthmus, the length of the snout, the over-all width of the mouth, the width of the cartilaginous ridge, and the length of the union of the lower lips. It is off-center in respect to the depth of the caudal peduncle and the length of the mouth (virtually insignificant characters in this comparison).

The hybridity of the available example is confirmed by the various features shared in general by the *Catostomus* × *Pantosteus* hybrids (pp. 33–36; Pl. VII, Figs. 3*a*–*c*). Its hybrid index is 44.

10. *Catostomus latipinnis discobolus* × *Pantosteus delphinus utahensis*

U.M.M.Z. No. 124767: 1 young 25 mm. long, collected by Carl L. Hubbs and family just above the mouth of a small tributary of Virgin River, immediately below mouth of La Verkin Creek, near La Verkin (Town 41 S., Range 13 W.), Utah; July 3, 1938.

TABLE XXIX

RELATIVE NUMBERS OF HYBRIDS, *Catostomus latipinnis discobolus* × *Pantosteus delphinus utahensis,* AND OF THE PARENTAL SPECIES

Specimens in University of Michigan Museum of Zoology	*Catostomus latipinnis discobolus*	Hybrid	*Pantosteus delphinus utahensis*
In collection containing hybrid U.M.M.Z. No. 124767	16	1	119
From the Virgin River system	125	1	590

This additional combination between a fine-scaled *Catostomus* and a *Pantosteus* falls in line with the other interspecific sucker hybrids in regard to the relationship between its characters and those of the parental species. The scales appear to be intermediate in number, but are too poorly developed

TABLE XXX

PROPORTIONATE MEASUREMENTS OF HYBRIDS BETWEEN *Catostomus latipinnis discobolus* AND *Pantosteus delphinus utahensis*, AND OF THE PARENTAL SPECIES

The measurements are expressed as thousandths of the standard length. There are given for each item the range of the measurements; the average, in parentheses; and, as a subscript, the number of specimens.

	Tributary of Virgin River, Utah	
Size group, mm.		
C. l. discobolus	…… $(35)_1$	89–105 $(97)_4$
Hybrid	…… $(25)_1$	…… ……
P. d. utahensis	30–35 $(33)_4$	…… $(89)_1$
Caudal peduncle, depth		
C. l. discobolus	…… (60)	58–63 (61)
Hybrid	…… (80)	…… ……
P. d. utahensis	75–84 (79)	…… (80)
Head length		
C. l. discobolus	…… (279)	254–272 (265)
Hybrid	…… (287)	…… ……
P. d. utahensis	281–299 (289)	…… (248)
Head depth		
C. l. discobolus	…… (168)	157–165 (160)
Hybrid	…… (168)	…… ……
P. d. utahensis	160–171 (168)	…… (146)
Head width		
C. l. discobolus	…… (151)	162–172 (165)
Hybrid	…… (162)	…… ……
P. d. utahensis	154–169 (167)	…… (162)
Isthmus width		
C. l. discobolus	…… (54)	53–57 (55)
Hybrid	…… (78)	…… ……
P. d. utahensis	83–103 (92)	…… (101)
Snout length		
C. l. discobolus	…… (105)	137–144 (139)
Hybrid	…… (107)	…… ……
P. d. utahensis	105–123 (117)	…… (107)

TABLE XXX—(*Cont.*)

PROPORTIONATE MEASUREMENTS OF HYBRIDS BETWEEN *Catostomus latipinnis discobolus* AND *Pantosteus delphinus utahensis*, AND OF THE PARENTAL SPECIES

The measurements are expressed as thousandths of the standard length. There are given for each item the range of the measurements; the average, in parentheses; and, as a subscript, the number of specimens.

	Tributary of Virgin River, Utah	
Mouth width		
C. l. discobolus	.... (89)	100–113 (105)
Hybrid	.... (86)	....
P. d. utahensis	91–124 (113)	.... (127)
Cartilaginous ridge, width		
C. l. discobolus	.... (38)	36–39 (37)
Hybrid	.... (48)	....
P. d. utahensis	53–62 (58)	.... (64)
Mouth length		
C. l. discobolus	.... (64)	82–88 (85)
Hybrid	.... (59)	....
P. d. utahensis	64–84 (75)	.... (91)
Lower lip, union		
C. l. discobolus	.... (13)	11–20 (16)
Hybrid	.... (19)	....
P. d. utahensis	24–31 (30)	.... (39)

in the one small example to be counted with accuracy. The dorsal rays (Table XXXII) number 11 instead of usually 13 or 14, as in the local stock of *C. l. discobolus*, or 9 or 10, as in *P. d. utahensis*.

Material for a comparison of the proportionate measurements (Table XXX) is very unsatisfactory. The most critical measurements, of the width of the isthmus and of the cartilaginous ridge, and of the length of the union of the lower lips, do exhibit the expected intermediacy. Under the circumstances the over-all width of the mouth does not. The other measurements are hardly critical enough to warrant consideration.

CONCLUSIONS

Although we miss the evidence of experimental matings and of cytological abnormalities that is available for other families of fishes, we feel that the data presented in this paper demonstrate that distinct species of the fish family Catostomidae do hybridize in nature. In general, the natural hybrids in this family seem to be of rather rare and sporadic occurrence (Table XXXI). The 182 hybrids identified in this family constitute 11.5 and 7.2 per cent of the specimens, respectively, of the more primitive and of the more specialized of the parental species with which they happened to be collected, but only 1.8 and 1.5 per cent of the specimens of the 2 species from the same river systems (as delimited in Table XXXI). If we could satisfactorily exclude the specimens that were taken in those parts of the river systems that are inhabited by only 1 of the species, the ratio of hybrid frequency would be raised somewhat. In those parts of the stated stream systems where both parental species occur, perhaps 1 sucker in 100 on the average is an int~~ra~~erspecific hybrid.

In 6 of the 10 crosses the frequency of hybridization is probably less than the average figures just given, but in 4 of the combinations, the hybrids seem to occur much more commonly. The hybrids between the not closely related species *Catostomus macrocheilus* and *C. syncheilus* (both subspecies) constitute 15.1 and 21.6 per cent of the individuals of the respective parental forms with which they were collected, and 6.4 and 4.2 per cent of the total numbers of the parental species at hand from the same river systems. In 2 combinations the hybrids are scarce in comparison with one of the parental species but, on the basis of the known material, actually seem in one cross to approximate and in the other to outnumber the second parental species, which is extremely rare in the same river system. There has obviously been in each case some extreme disruption of the normal ecological relationships. In one of the combinations we can feel reasonably sure that the basis for the anomalous mating relationship was the recent introduction of one of the forms, *Catostomus commersonnii sucklii,* into the Colorado River system, where *Pantosteus d. delphinus,* the other parental species, abounds. In the other similar situation, we can explain the extreme rarity of one parental species (*Catostomus,* species) as due either to its recent introduction, or, more plausibly, to the destruction of its former habitat, following the use of the stream water for irrigation. On either basis, this rare form would have been forced into association with an abundance of another species, *Pantosteus santa-anae,* with which most of its few spawners would appear to have hybridized. In this situation the rare species appears from observation as well as on theoretical grounds to be approaching extinction. The 2 specimens of *Catostomus* and the 38 hybrids collected on October 2, 1942, showed gonadal evidence of having spawned little to not at all during the preceding spawning season. In this combination the sex ratio may be somewhat disturbed.

The rare and sporadic occurrence of specimens unclassifiable as to species, except where the normal population ratios have been greatly disturbed as just indicated, is a main reason for the interpretation of the aberrant individuals as hybrids. The presumed parental species are known to occur in the same system and have generally been collected with the fish thought

TABLE XXXI

SUMMARY DATA ON RELATIVE NUMBERS OF CATOSTOMID HYBRIDS AND OF THE PARENTAL KINDS

Derived from Tables I, IV, IX, XIII, XV, XVII, XX, XXIV, XXVII, and XXIX. See these tables for further details and for qualifying remarks.

Hybrid Combination	River System	More Primitive Parental Species (Coarse-scaled *Catostomus* in *Catostomus* × *Catostomus* Crosses, or Any *Catostomus* in the *Catostomus* × *Pantosteus* Combinations)		Hybrids	More Specialized Parental Species (Fine-scaled *Catastomus* in *Catostomus* × *Catostomus* Crosses, or *Pantosteus* Species in the *Catostomus* × *Pantosteus* Combinations)	
		Collected in Same River System	Collected with Hybrids		Collected with Hybrids	Collected in Same River System
Catostomus commersonnii sucklii *Catostomus catostomus griseus*	Platte	1250	169	5	41	692
Catostomus macrocheilus *Catostomus syncheilus syncheilus*	Columbia (Palouse excepted)	969	384	69	273	1341*
Catostomus macrocheilus *Catostomus syncheilus palouseanus*	Palouse (Washington)	152	93	3	60	358
Catostomus commersonnii sucklii *Pantosteus jordani*	Missouri	2111†	47	2	44	691
Catostomus commersonnii sucklii *Pantosteus delphinus delphinus*	Colorado	10	1	7	34	2031
Catostomus insignis *Pantosteus clarkii*	Gila (Arizona)	1256	349	21	416	2069
Catostomus, species *Pantosteus santa-anae*	Santa Clara (California)	5	4	44	825	1907
Catostomus tahoensis *Pantosteus lahontan*	Lahontan	3282	500	28	677	2007
Catostomus catostomus griseus *Pantosteus jordani*	Platte	692	15	2	56	81
Catostomus latipinnis discobolus *Pantosteus delphinus utahensis*	Virgin (Utah, etc.)	125	16	1	119	590
Totals	All named	9852†	1578	182	2545	11767‡

* Including some specimens probably referable to other subspecies.

† Including the 1250 specimens of *Catostomus commersonnii sucklii* from the Platte River System, enumerated also in the count for the Missouri System.

‡ Including the 692 specimens of *Catostomus catostomus griseus*, enumerated also as the more primitive species in another combination.

to be hybrids. No integrity of populations or of spawning runs, or other evidence of specific integrity, has been indicated for the aberrant types. Their characters, particularly in the intergeneric crosses, *Catostomus* × *Pantosteus,* are discordant with the taxonomic system of the family. Nor do they have features which would lead one to regard them as extreme variants or mutant sports of any recognized species. No assumption other than that of the intermating of species in nature agrees with the facts.

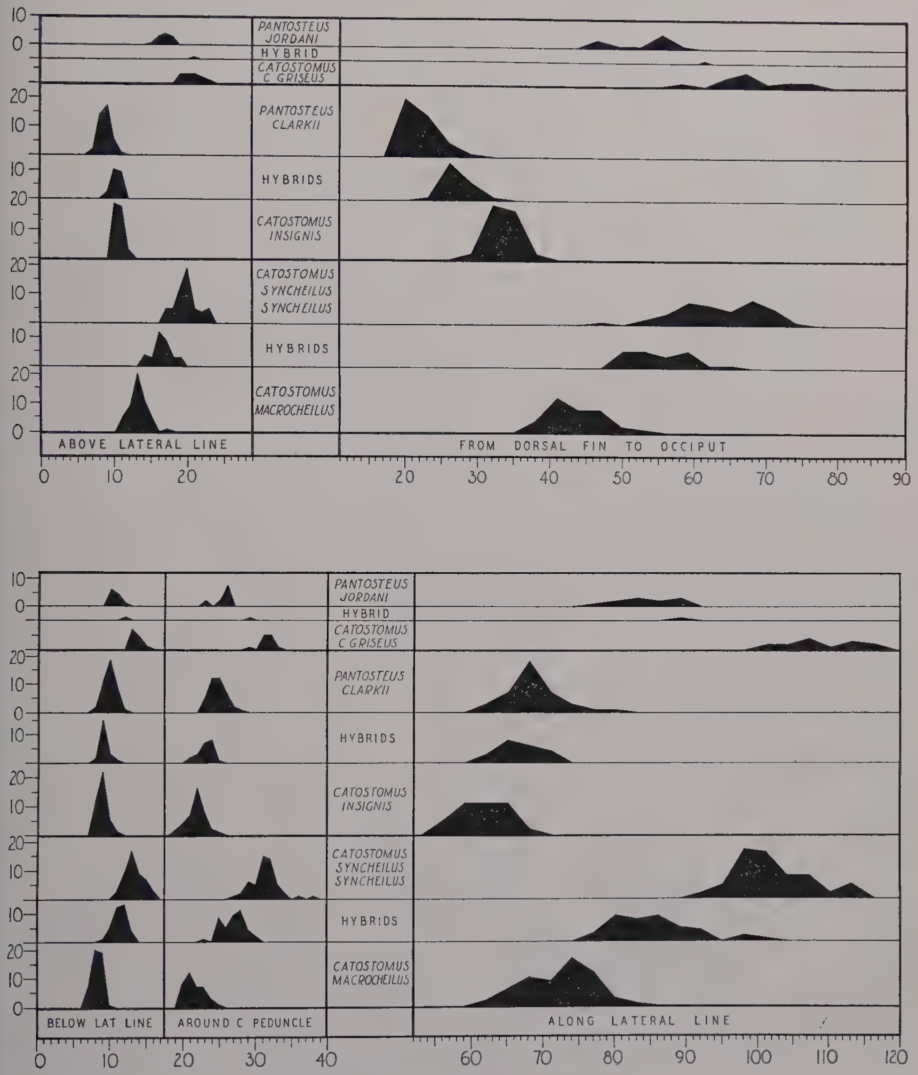

FIG. 7. Comparison of various sucker hybrids with their parental species in the 5 scale counts (Tables XXXIII–XXXVII).

The most cogent reason that favors the hypothesis of hybridity is that

TABLE XXXII

NUMBER OF DORSAL RAYS IN SUCKER HYBRIDS AND IN PARENTAL SPECIES

	Number of Dorsal Rays								Statistical Computations					
	9	10	11	12	13	14	15	16	No.	Range	Ave.	S.E.	V	Hybrid Index
Catostomus commersonnii sucklii	......	......	23	7	......	......	......	......	30	11–12	11.23	.08	3.9	......
Hybrids	......	3	2	......	......	......	......	......	5	10–11	10.40	.24	5.2	69
Catostomus catostomus griseus	1	33	......	1	......	......	......	......	35	9–12	10.03	.06	3.5	......
Catostomus macrocheilus	......	......	......	2	24	37	12	1	76	12–16	13.82	.09	5.7	......
Hybrids	......	......	1	27	34	6	......	......	68	11–14	12.66	.08	5.2	64
Catostomus syncheilus syncheilus	......	......	17	46	17	......	......	......	80	11–13	12.00	.07	5.2	......
Catostomus macrocheilus	......	......	......	6	21	23	......	......	50	12–14	13.34	.10	5.3	......
Hybrids	......	......	......	2	1	......	......	......	3	12–13	12.33	.33	4.6	46
Catostomus syncheilus palouseanus	......	3	30	9	......	......	......	......	42	10–12	11.14	.08	4.65	......
Catostomus commersonnii sucklii	......	......	9	1	......	......	......	......	10	11–12	11.10	.10	2.85	......
Hybrids	......	1	1	......	......	......	......	......	2	10–11	10.50?		...	86?
Pantosteus jordani	......	6	4	......	......	......	......	......	10	10–11	10.40	.16	4.9	......
*Catostomus commersonnii sucklii**	......	......	29	8	......	......	......	......	37	11–12	11.22	.07	3.8	......
Hybrids	......	3	4	......	......	......	......	......	7	10–11	10.57	.14	3.5	88
Pantosteus delphinus delphinus	......	13	12	......	......	......	......	......	25	10–11	10.48	.10	4.8	......
Catostomus insignis	......	......	27	13	......	......	......	......	40	11–12	11.33	.07	3.9	......
Hybrids	......	3	15	3	......	......	......	......	21	10–12	11.00	.12	5.0	45
Pantosteus clarkii	......	16	23	......	......	......	......	......	39	10–11	10.59	.08	4.7	......
Catostomus, species	......	3	2	......	......	......	......	......	5	10–11	10.40	.24	4.6	......
Hybrids	2	30	12	......	......	......	......	......	44	9–11	10.23	.08	5.2	40
Pantosteus santa-anae†	13	190	9	......	......	......	......	......	212	9–11	9.98	.02	2.9	......
Catostomus tahoensis	1	165	95	4	......	......	......	......	265	9–12	10.38	.03	5.05	......
Hybrids	......	20	7	1	......	......	......	......	28	10–12	10.32	.10	5.2	21
Pantosteus lahontan	3	186	25	......	......	......	......	......	214	9–11	10.10	.02	3.4	......
Catostomus catostomus griseus	4	8	......	......	......	......	......	......	12	9–10	9.67	.14	5.0	......
Hybrid	......	1	......	......	......	......	......	......	1	10	10.00?			137?
Pantosteus jordani	2	8	1	......	......	......	......	......	11	9–11	9.91	.16	5.4	......
Catostomus latipinnis discobolus	......	......	......	......	3	2	......	......	5	13–14	13.40	.24	4.0	......
Hybrid	......	......	1	......	......	......	......	......	1	11	11.00?			63?
Pantosteus delphinus utahensis	2	3	......	......	......	......	......	......	5	9–10	9.60	.24	5.6	......

* Including the counts listed in the top row.

† Of the 212 counts, 168 were furnished by Robert R. Miller.

TABLE XXXIII

Number of Lateral Line Scales in Sucker Hybrids and in Parental Species

	Number of Lateral Line Scales (Frequencies)																								Statistical Computations					
	55–57	58–60	61–63	64–66	67–69	70–72	73–75	76–78	79–81	82–84	85–87	88–90	91–93	94–96	97–99	100–102	103–105	106–108	109–111	112–114	115–117	118–120	121–123	124–126	No.	Range*	Ave.*	S.E.*	V*	Hybrid Index
commersonnii sucklii	9	12	2	4	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	27	55–65	59.11	.59	5.2	
ybrids	......	......	......	......	......	1	1	2	......	......	1	......	......	......	......	......	......	......	......	......	......	......	......	......	5	72–87	77.00	2.51	7.3	42
catostomus griseus	......	......	......	......	......	......	......	......	......	......	3	2	4	1	3	1	4	3	2	5	2	1	......	......	31	86–118	102.16	1.83	10.0	....
macrocheilus	......	......	2	6	10	9	12	7	3	1	......	......	......	......	......	......	......	......	......	......	......	......	......	......	50	61–83	71.66	.70	6.9	..
ybrids	......	......	......	......	......	......	......	3	9	8	9	5	4	......	2	1	......	......	......	......	......	......	......	......	41	76–100	85.34	.90	6.75	45
syncheilus syncheilus	......	......	......	......	......	......	......	......	......	......	......	......	1	5	17	16	8	8	2	5	......	......	......	......	62	93–113	101.97	.65	5.0	......
macrocheilus	......	......	......	......	4	4	16	9	3	......	2	......	1	......	......	......	......	......	......	......	......	......	......	......	39	67–93	75.31	.79	6.55	....
ybrids	......	......	......	......	......	......	......	......	......	......	1	......	......	......	1	......	......	......	......	......	......	......	......	......	2	85–99	92.0?	......	..	56?
syncheilus palouseanus	......	......	......	......	......	......	......	......	......	......	......	1	......	1	2	7	11	7	7	1	1	......	......	1	39	90–124	105.23	.96	5.7	......
ommersonnii sucklii	2	2	5	1	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	10	56–64	60.50	.92	10.0	......
brids	......	......	......	......	1	......	......	1	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	2	67–77	72.5?	......	..	45?
jordani	......	......	......	......	......	......	......	2	......	2	1	2	1	1	1	......	......	......	......	......	......	......	......	......	10	78–97	86.90	2.11	7.7	......
commersonnii sucklii†	9	13	4	6	2	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	34	55–68	60.12	.59	5.7	......
ybrids	......	......	1	......	......	1	1	......	......	1	......	1	......	......	1	1	......	......	......	......	......	......	......	......	7	63–100	82.29	5.43	17.5	52
delphinus delphinus	......	......	......	......	......	......	......	......	......	1	......	1	......	2	4	3	3	8	2	......	......	1	......	......	25	84–118	102.36	1.43	7.0	......
insignis	5	11	11	11	2	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	40	56–67	61.55	.53	5.45	.....
ybrids	......	......	3	8	6	4	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	21	61–70	66.57	.64	4.4	72
clarkii	......	......	3	7	18	7	3	1	1	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	40	61–79	68.53	.60	5.5	......
atostomus, species	......	......	......	......	1	......	1	......	......	1	1	1	......	......	......	......	......	......	......	......	......	......	......	......	5	69–88	80.40	3.61	9.0	.....
ybrids	......	......	......	1	......	1	9	11	9	9	3	1	......	......	......	......	......	......	......	......	......	......	......	......	44	66–89	78.57	.68	5.8	73
santa-anae	......	......	......	......	1	......	10	13	17	4	1	......	......	......	......	......	......	......	......	......	......	......	......	......	46	69–87	77.89	.47	4.1	......
tahoensis	......	......	......	......	......	......	......	......	1	2	2	3	5	......	......	......	......	......	......	......	......	......	......	......	13	80–93	88.08	1.15	8.8	......
ybrids	......	......	......	......	......	......	1	1	......	3	......	1	3	......	......	......	......	......	......	......	......	......	......	......	9	73–92	85.15	2.05	7.2	60
lahontan	......	......	......	......	......	1	......	6	6	4	3	3	2	1	1	......	......	......	......	......	......	......	......	......	27	72–99	83.22	1.24	7.7	......
catostomus griseus	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	1	1	4	1	3	2	......	......	......	12	102–117	109.50	1.37	4.3	......
ybrid	......	......	......	......	......	......	......	......	......	......	......	1	......	......	......	......	......	......	......	......	......	......	......	......	1	90	90.0?	......	......	77?
jordani	......	......	......	......	......	......	......	1	2	3	2	3	......	......	......	......	......	......	......	......	......	......	......	......	11	77–89	84.09	1.23	4.85	......

* Computed from the original, unclassed data.
† Including the counts listed in the top row.

TABLE XXXIV

Number of Predorsal Scales in Sucker Hybrids and in Parental Species

	Number of Predorsal Scales (Frequencies)																				Statistical Computations					
	19–21	22–24	25–27	28–30	31–33	34–36	37–39	40–42	43–45	46–48	49–51	52–54	55–57	58–60	61–63	64–66	67–69	70–72	73–75	76–78	No.	Range*	Ave.*	S.E.*	V*	Hybrid Index
C. commersonnii sucklii	......	......	......	3	13	6	3	......	......	......	......	......	......	......	......	......	......	......	......	......	25	28–39	33.08	.52	7.9	......
Hybrids	......	......	......	......	......	......	......	......	1	1	1	......	......	......	......	......	......	......	......	......	3	45–49	47.00	1.73	6.4	52
C. catostomus griseus	......	......	......	......	......	......	......	......	......	4	1	1	3	6	4	8	2	......	1	......	30	46–73	59.70	1.27	11.65	......
C. macrocheilus	......	......	......	......	......	......	4	12	8	8	2	1	......	......	......	......	......	......	......	......	35	37–53	43.57	.63	8.55	......
Hybrids	......	......	......	......	......	......	......	......	......	......	6	6	4	6	1	1	......	......	......	......	24	49–64	55.13	.87	7.7	59
C. syncheilus syncheilus	......	......	......	......	......	......	......	......	......	1	......	2	4	8	7	5	9	6	1	......	43	46–75	63.26	.92	9.5	......
C. macrocheilus	......	......	......	......	......	1	2	10	11	5	......	......	......	......	......	......	......	......	......	......	29	36–48	42.76	.55	6.9	......
Hybrids	......	......	......	......	......	......	......	......	......	......	......	......	1	......	......	1	......	......	......	......	2	56–65	60.5?	......	. .	82?
C. syncheilus palouseanus	......	......	......	......	......	......	......	......	......	......	......	......	1	4	9	7	4	4	1	......	30	56–74	64.50	.80	6.8	......
C. commersonnii sucklii	......	......	......	......	1	7	2	......	......	......	......	......	......	......	......	......	......	......	......	......	10	33–38	35.30	.54	4.8	......
Hybrids	......	......	......	......	......	......	......	1	......	1	......	......	......	......	......	......	......	......	......	......	2	40–47	45.0?	......	. . .	50?
P. jordani	......	......	......	......	......	......	......	......	......	1	1	3	2	2	1	......	......	......	......	......	10	48–61	54.80	1.43	8.25	......
C. commersonnii sucklii†	......	......	......	3	13	13	3	......	......	......	......	......	......	......	......	......	......	......	......	......	32	28–39	33.47	.46	7.8	......
Hybrids	......	......	......	......	......	......	1	1	......	1	1	......	1	......	......	......	......	......	......	......	5	39–57	46.40	3.28	15.8	50
P. delphinus delphinus	......	......	......	......	......	......	......	......	......	......	1	2	4	4	4	5	......	......	......	......	20	49–66	59.45	.99	7.45	......
C. insignis	......	......	......	2	19	17	2	......	......	......	......	......	......	......	......	......	......	......	......	......	40	30–37	33.43	.32	6.05	......
Hybrids	......	1	13	6	1	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	21	24–31	27.00	.43	7.3	56
P. clarkii	20	14	5	1	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	40	19–28	22.03	.38	10.9	......
Catostomus, species	......	......	......	......	......	......	......	2	3	......	......	......	......	......	......	......	......	......	......	......	5	40–45	42.80	.86	4.0	......
Hybrids	......	......	......	......	......	......	7	24	12	1	......	......	......	......	......	......	......	......	......	......	44	38–46	41.55	.29	4.7	35
P. santa-anae	......	......	......	......	......	8	14	19	5	......	......	......	......	......	......	......	......	......	......	......	46	34–44	39.24	.39	6.7	......
C. tahoensis	......	......	......	......	......	......	......	1	1	4	5	2	1	......	......	......	......	......	......	......	14	42–55	48.93	1.02	7.8	......
Hybrids	......	......	......	......	......	......	......	......	3	3	1	......	1	1	......	......	......	......	......	......	9	44–58	48.56	1.68	10.4	116
P. lahontan	......	......	......	......	......	......	......	......	6	10	5	6	......	1	......	......	......	......	......	......	28	43–58	48.61	.72	7.8	......
C. catostomus griseus	......	......	......	......	......	......	......	......	......	......	......	......	......	1	......	3	5	1	1	1	12	60–76	68.00	1.33	6.8	......
Hybrid	......	......	......	......	......	......	......	......	......	......	......	......	......	......	1	......	......	......	......	......	1	61	61.0?	......	......	47?
P. jordani	......	......	......	......	......	......	......	......	......	3	1	1	5	1	......	......	......	......	......	......	11	46–59	53.00	1.34	8.4	......

* Computed from original, unclassed data.
† Including the counts listed in the top row.

TABLE XXXV

Number of Scales above the Lateral Line in Sucker Hybrids and in Parental Species

	Number of Scales above the Lateral Line (Frequencies)																					Statistical Computations					
	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	No.	Range	Ave.	S.E.	V	Hybrid Index
. *commersonnii sucklii*	......	......	5	15	6	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	26	9–11	10.04	.13	6.5	......
ybrids	......	......	......	......	......	1	1	......	......	1	1	......	......	......	......	......	......	......	......	......	......	4	12–17	14.50	1.19	16.4	52
. *catostomus griseus*	......	......	......	......	......	......	......	......	......	4	2	7	7	6	1	2	......	......	......	......	......	29	16–22	18.69	.31	8.9	......
. *macrocheilus*	......	......	......	......	5	9	20	11	5	......	1	......	......	......	......	......	......	......	......	......	......	51	11–17	13.12	.17	9.25	......
ybrids	......	......	......	......	......	......	......	4	3	12	9	3	3	......	......	......	......	......	......	......	......	34	14–19	16.38	.24	8.5	48
. *syncheilus syncheilus*	......	......	......	......	......	......	......	......	......	......	5	5	11	19	5	4	5	......	......	......	......	54	17–23	19.85	.22	8.1	......
. *macrocheilus*	......	......	......	......	2	5	16	13	2	1	1	......	......	......	......	......	......	......	......	......	......	40	11–17	13.37	.18	8.5	......
ybrids	......	......	......	......	......	......	......	......	......	......	......	1	1	......	......	......	......	......	......	......	......	2	18–19	18.5?	......	......	62?
. *syncheilus palouseanus*	......	......	......	......	......	......	......	......	......	1	......	1	2	5	11	5	6	2	3	......	1	37	16–27	21.65	.35	9.8	......
. *commersonnii sucklii*	......	......	2	5	3	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	10	9–11	10.10	.23	7.2	......
ybrids	......	......	......	......	......	......	2	......	......	......	......	......	......	......	......	......	......	......	......	......	......	2	13–13	13.0?	......	......	38?
. *jordani*	......	......	......	......	......	......	......	......	......	2	2	3	2	1	......	......	......	......	......	......	......	10	16–20	17.80	.42	7.5	......
. *commersonnii sucklii**	......	......	5	19	9	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	33	9–11	10.12	.11	6.3	......
ybrids	......	......	......	......	3	......	......	1	2	1	......	......	......	......	......	......	......	......	......	......	......	7	11–16	13.29	.84	16.7	62
. *delphinus delphinus*	......	......	......	......	......	......	......	......	......	2	5	2	3	3	4	1	......	......	......	......	......	20	16–22	18.80	.41	9.75	......
. *insignis*	......	......	......	19	18	3	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	40	10–12	10.60	.10	6.0	......
ybrids	......	......	2	10	9	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	21	9–11	10.33	.14	6.2	15
. *clarkii*	2	14	17	6	1	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	40	7–11	8.75	.14	10.1	......
atostomus, species	......	......	......	......	......	......	1	......	2	2	......	......	......	......	......	......	......	......	......	......	......	5	13–16	15.00	.58	7.7	......
ybrids	......	......	......	......	......	......	......	7	19	13	5	......	......	......	......	......	......	......	......	......	......	44	14–17	15.36	.13	5.7	– 34
. *santa-anae*	......	......	......	......	......	......	17	17	10	2	......	......	......	......	......	......	......	......	......	......	......	46	13–16	13.93	.09	4.2	......
. *tahoensis*	......	......	......	......	......	......	......	......	1	4	4	3	2	......	......	......	......	......	......	......	......	14	15–19	17.07	.32	7.0	......
Hybrids	......	......	......	......	......	......	......	......	......	4	4	1	......	......	......	......	......	......	......	......	......	9	16–18	16.67	.24	4.3	23
. *lahontan*	......	......	......	......	......	......	4	4	4	11	4	1	......	......	......	......	......	......	......	......	......	28	13–18	15.36	.26	9.0	......
. *catostomus griseus*	......	......	......	......	......	......	......	......	......	......	......	......	3	3	3	2	1	......	......	......	......	12	19–23	20.58	.37	6.2	......
Hybrid	......	......	......	......	......	......	......	......	......	......	......	......	......	......	1	......	......	......	......	......	......	1	21	21.0?	......	......	– 11?
. *jordani*	......	......	......	......	......	......	......	......	1	3	4	3	......	......	......	......	......	......	......	......	......	11	15–18	16.82	.30	5.9	......

* Including the counts listed in the top row.

TABLE XXXVI

NUMBER OF SCALES BELOW THE LATERAL LINE IN SUCKER HYBRIDS AND IN PARENTAL SPECIES

	Scales below Lateral Line (Frequencies)											Statistical Computations					
	7	8	9	10	11	12	13	14	15	16	17	No.	Range	Ave.	S.E.	V	Hybrid Index
C. commersonnii sucklii	15	11	1	......	......	......	......	......	......	......	......	27	7–9	7.48	.11	7.6	......
Hybrids	......	1	......	1	2	......	......	......	......	......	......	4	8–11	10.00	.71	14.2	63
C. catostomus griseus	......	......	2	7	8	10	4	......	2	......	......	33	9–15	11.45	.25	12.5	......
C. macrocheilus	8	20	19	1	......	......	......	......	......	......	......	48	7–10	8.27	.11	9.2	......
Hybrids	......	......	1	5	12	13	4	......	......	......	......	35	9–13	11.40	.16	8.3	62
C. syncheilus syncheilus	......	......	......	......	3	9	17	9	7	3	......	48	11–16	13.35	.19	9.9	......
C. macrocheilus	1	9	23	5	2	......	......	......	......	......	......	40	7–11	8.95	.13	9.2	......
Hybrids	......	1	......	......	2	......	......	......	......	......	......	3	8–11	10.0?	1.00	17.3?	19?
C. syncheilus palouseanus	......	......	......	......	1	2	2	15	11	7	3	41	11–17	14.61	.22	9.6	......
C. commersonnii sucklii	4	6	......	......	......	......	......	......	......	......	......	10	7–8	7.60	.16	6.7	......
Hybrids	......	2	......	......	......	......	......	......	......	......	......	2	8–8	8.0?	..	..	12?
P. jordani	......	......	1	1	5	3	......	......	......	......	......	10	9–12	11.00	.30	9.6	......
*C. commersonnii sucklii**	16	17	1	......	......	......	......	......	......	......	......	34	7–9	7.56	.10	7.7	......
Hybrids	......	1	2	......	3	1	......	......	......	......	......	7	8–12	10.14	.55	14.35	49
P. delphinus delphinus	......	......	......	5	2	2	2	3	3	3	......	20	10–16	12.85	.50	17.4	......
C. insignis	......	12	22	5	1	......	......	......	......	......	......	40	8–11	8.88	.11	7.8	......
Hybrids	......	2	15	3	1	......	......	......	......	......	......	21	8–11	9.14	.14	7.0	26
P. clarkii	......	2	11	18	8	1	......	......	......	......	......	40	8–12	9.88	.14	9.0	......
Catostomus, species	......	......	......	......	1	3	1	......	......	......	......	5	11–13	12.00	.32	5.3	......
Hybrids	......	......	......	......	3	9	16	12	3	1	......	44	11–16	13.14	.17	8.4	139
P. santa-anae	......	......	......	......	4	11	9	5	4	......	......	33	11–15	12.82	.21	9.3	......
C. tahoensis	......	......	......	4	4	7	3	2	......	......	......	20	10–14	11.75	.28	10.7	......
Hybrids	......	......	1	3	4	1	1	......	......	......	......	10	9–13	10.80	.34	9.95	52
P. lahontan	......	2	7	2	1	3	1	......	......	......	......	16	8–13	9.94	.19	7.65	......
C. catostomus griseus	......	......	......	......	......	......	7	4	1	......	......	12	13–15	13.50	.18	4.6	......
Hybrid	......	......	......	......	......	1	......	......	......	......	......	1	12	12.0?	..	......	51?
P. jordani	......	......	......	6	4	1	......	......	......	......	......	11	10–12	10.55	.20	6.3	......

* Including the counts listed in the top row.

TABLE XXXVII

NUMBER OF SCALES AROUND THE CAUDAL PEDUNCLE IN SUCKER HYBRIDS AND IN PARENTAL SPECIES

	Number of Scales around Caudal Peduncle (Frequencies)																					Statistical Computations					
	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	No.	Range	Ave.	S.E.	V	Hybrid Index
C. commersonnii sucklii	......	7	11	5	2	2	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	27	19–23	20.30	.23	5.9	......
Hybrids	......	......	......	......	......	......	......	......	......	1	2	1	......	......	......	......	......	......	......	......	......	4	27–29	28.00	.41	2.9	72
C. catostomus griseus	......	......	......	......	......	......	......	......	1	1	3	4	3	6	8	4	1	1	1	......	......	33	26–36	30.97	.39	7.2	......
C. macrocheilus	3	4	15	13	9	3	1	......	......	......	......	......	......	......	......	......	......	......	......	......	......	48	18–24	20.71	.19	6.4	......
Hybrids	......	......	......	......	......	1	......	8	5	9	11	4	2	......	......	......	......	......	......	......	......	40	23–30	27.00	.25	5.9	59
C. syncheilus syncheilus	......	......	......	......	......	......	......	......	......	1	2	6	5	15	14	5	2	......	1	......	1	52	27–38	31.29	.26	6.0	......
C. macrocheilus	......	......	8	12	7	7	3	1	......	......	......	......	......	......	......	......	......	......	......	......	......	38	20–25	21.68	.22	6.25	......
Hybrids	......	......	......	......	......	......	......	......	1	......	1	......	......	......	......	......	......	......	......	......	......	2	26–28	27.0?	......	......	49?
C. syncheilus palouseanus	......	......	......	......	......	......	......	......	......	......	......	......	7	10	5	6	4	4	1	2	1	40	30–38	32.55	.35	6.8	......
C. commersonnii sucklii	1	3	2	3	1	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	10	18–22	20.00	.39	6.2	......
Hybrids	......	......	......	......	......	......	1	1	......	......	......	......	......	......	......	......	......	......	......	......	......	2	24–25	24.5?	......	......	58?
P. jordani	......	......	......	......	......	......	......	......	2	2	3	3	......	......	......	......	......	......	......	......	......	10	26–29	27.70	.37	4.2	......
*C. commersonnii sucklii**	1	7	17	5	2	2	......	......	......	......	......	......	......	......	......	......	......	......	......	......	......	34	18–23	20.18	.19	5.5	......
Hybrids	......	......	......	......	1	2	......	......	......	2	1	......	1	......	......	......	......	......	......	......	......	7	22–30	25.71	1.14	11.7	64
P. delphinus delphinus	......	......	......	......	......	......	......	1	1	5	3	6	1	3	3	......	......	......	......	......	......	23	25–32	28.83	.42	7.0	......
C. insignis	......	2	4	7	16	8	2	1	......	......	......	......	......	......	......	......	......	......	......	......	......	40	19–25	21.85	.20	5.8	......
Hybrids	......	......	......	2	3	7	8	1	......	......	......	......	......	......	......	......	......	......	......	......	......	21	21–25	23.14	.23	4.6	44
P. clarkii	......	......	......	......	......	5	12	12	7	2	1	......	......	......	......	......	......	......	......	......	......	39	23–28	24.79	.19	4.8	......
Catostomus, species	......	......	......	......	......	......	......	1	1	1	2	......	......	......	......	......	......	......	......	......	......	5	25–28	26.80	.58	4.35	......
Hybrids	......	......	......	......	......	......	......	3	2	10	14	8	7	......	......	......	......	......	......	......	......	44	25–30	27.98	.20	4.85	48
P. santa-anae	......	......	......	......	......	......	......	......	......	6	5	12	17	5	1	......	......	......	......	......	......	46	27–32	29.28	.18	4.25	......
C. tahoensis	......	......	......	......	......	......	......	......	......	......	......	1	4	6	2	1	......	......	......	......	......	14	29–33	30.86	.27	3.3	......
Hybrids	......	......	......	......	......	......	......	......	2	1	3	3	......	......	......	......	......	......	......	......	......	9	26–29	27.78	.40	4.3	60
P. lahontan	......	......	......	......	......	2	5	6	4	8	3	......	......	......	......	......	......	......	......	......	......	28	23–28	25.71	.29	6.0	......
C. catostomus griseus	......	......	......	......	......	......	......	......	......	......	......	1	......	5	5	1	......	......	......	......	......	12	29–33	31.42	.29	3.2	......
Hybrid	......	......	......	......	......	......	......	......	......	......	......	1	......	......	......	......	......	......	......	......	......	1	29	29.0?	......	......	39?
P. jordani	......	......	......	......	......	2	......	2	7	......	......	......	......	......	......	......	......	......	......	......	......	11	23–26	25.27	.36	4.7	......

* Including the counts listed in the top row.

the aberrant specimens are uniformly intermediate between the species which logically may be assumed to be parental. This basis for the identification of natural hybrids has already been treated (pp. 12–14). We point out now how well the data for the Catostomidae conform with the general observation that, in fishes at least, systematic characters usually exhibit a seemingly almost Galtonian type of inheritance.

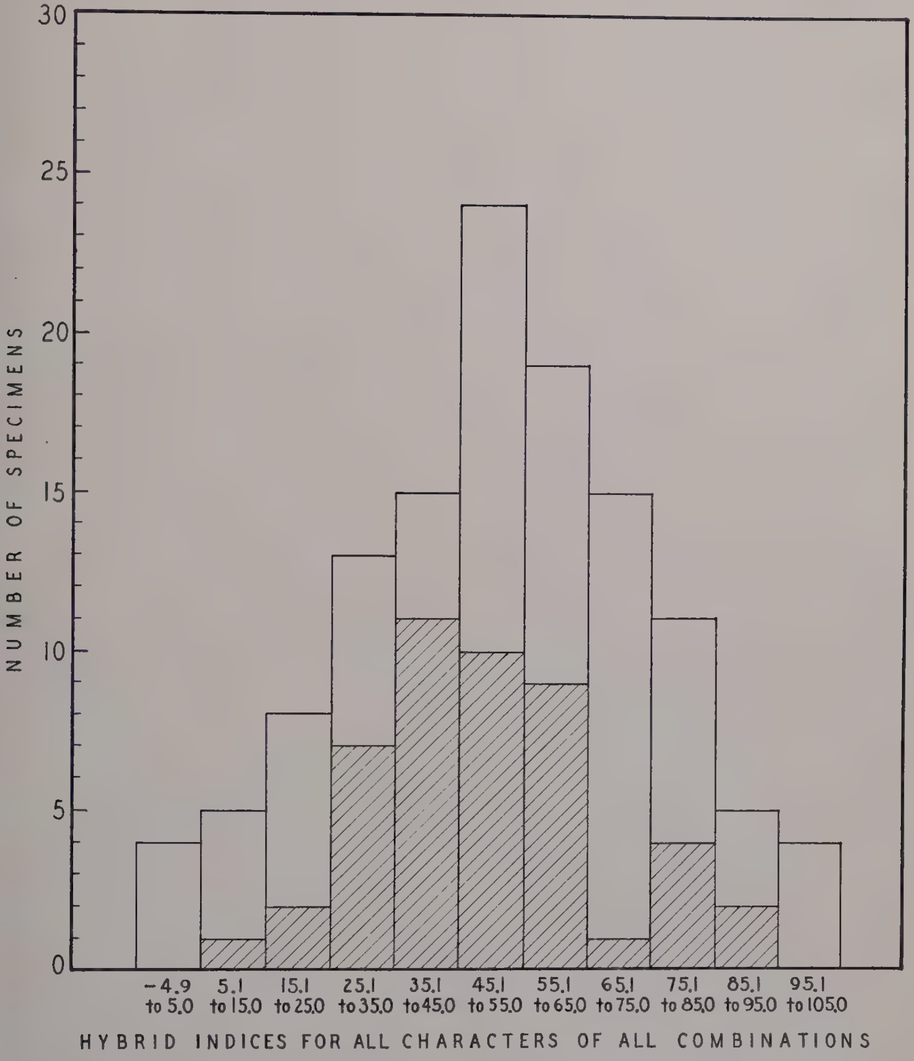

FIG. 8. Histogram showing frequency distribution of the average hybrid index for each hybrid specimen (Table XXXIX).

Shaded rectangles represent *Catostomus* × *Pantosteus* hybrids; the hollow blocks, *Catostomus* × *Catostomus* crosses. The concordant data of 1942 for the *Catostomus*, species × *Pantosteus santa-anae* cross and 18 dorsal ray counts for *Catostomus tahoensis* × *Pantosteus lahontan* were added to the text after the graph was drawn.

Whenever there is a marked and trustworthy difference between the parental species in the number of dorsal rays, the averages for the hybrids intervene nicely between the means for the parental species (Table XXXII). This is also true for the number of scales in each of the 5 series counted (Tables XXXIII–XXXVII; Fig. 7.) In 3 of the combinations the pelvic rays were found to average fewer than in one species but more than in the other (Tables VIII and XXVI).

The proportionate measurements of the hybrids, in general, also intervene between those of the parent forms (Tables II, VI, X, XIV, XVI, XIX, XXII, XXV, XXVIII, and XXX). The evidence is not quite so clear as for the counts, in our opinion principally for the reason that the measurement data need to be separated by localities and size groups, thus greatly restricting the size of each unit of comparison. Even so, the average values are intermediate in the hybrids for almost all the proportions in which the species involved show any considerable difference.

The intermediacy of the hybrids is exhibited also in many features of form and coloration, as outlined through the text and as illustrated in Plates III–VII. As compared with its mate in miscegenation, one of the parental species usually has a larger, more depressed, more bulbous snout, that projects farther beyond the more inferior mouth, and the hybrid is in between. Usually, one of the species is darker and more strongly mottled than the other species, and the hybrid again forms a graded series with its parents. In the *Catostomus commersonnii sucklii* × *Catostomus catostomus griseus* cross, intermediate life colors were also observed (p. 19). In one of the *Catostomus* × *Pantosteus* combinations the hybrids were seen to be intermediate in developmental features of pigmentation (pp. 57–58).

The position of the hybrids between the parental species is strikingly brought out by certain character indices (the use of the character index is explained and justified on pp. 4–6). Indices which sharpen the expression of difference between the species and emphasize the intermediacy of the hybrids are as follows:

> Sum of all scale counts minus number of dorsal rays, for the *Catostomus macrocheilus* × *C. syncheilus* combinations (Table V; Fig. 1).
>
> Sum of 3 scale counts minus sum of the other 2 scale counts, for the *Catostomus insignis* × *Pantosteus clarkii* cross (Table XVIII; Fig. 5).
>
> Distance from dorsal fin to occiput divided by length of depressed dorsal fin, for the *macrocheilus* × *syncheilus* series (Table VII; Fig. 2).
>
> Sum of several proportionate measurements of mouth and isthmus (Table XI; Figs. 3–4).

The hybrid indices (pp. 6–8) tend to approximate very closely the value 50, which is the indication of exact intermediacy on a percentage scale, in which the mean value for one parental type is set at 0 and that of the other species at 100. The hybrid indices for the several characters yield a grand average of 51 (Table XXXVIII). The hybrid indices for the charac-

TABLE XXXVIII

FREQUENCIES OF INDIVIDUAL HYBRID INDICES, FOR ALL COMBINATIONS BETWEEN SPECIES OF *Catostomus* AND BETWEEN THOSE OF *Catostomus* AND *Pantosteus*, AND FOR ALL LOCALITIES

An index of 50 indicates exact intermediacy, on a scale in which the average value for the more primitive parental species is set at 0, and that for the more specialized parental species at 100. Indices are disregarded when the difference between the parental species is less than 4 per cent.

Character and Combination	Average Difference between Parent Species*		Individual Hybrid Indices									No.	Ave.†
	Amount	Per Cent	< −37.5	−37.5 to −12.5	−12.5 to 12.5	12.5 to 37.5	37.5 to 62.5	62.5 to 87.5	87.5 to 112.5	112.5 to 137.5	> 137.5		
Dorsal rays													
Catostomus × *Catostomus*	1.8	13	......	......	6	3	36	......	30	......	1	76	63
Catostomus × *Pantosteus*	1.0	5	15	......	......	5	15	1	30	......	9	75	51
Lateral line scales													
Catostomus × *Catostomus*	31.6	45	......	......	......	19	20	7	2	......	......	48	47
Catostomus × *Pantosteus*	8.1	12	4	......	4	8	6	8	5	4	7	46	73
Predorsal scales													
Catostomus × *Catostomus*	20.5	49	......	......	......	5	12	10	2	......	......	29	59
Catostomus × *Pantosteus*	7.2	20	3	6	3	12	23	18	6	2	......	73	43
Scales above lateral line													
Catostomus × *Catostomus*	7.0	55	......	......	......	9	23	8	......	......	......	40	49
Catostomus × *Pantosteus*	2.2	18	19	25	8	13	5	7	7	......	......	84	−8
Scales below lateral line													
Catostomus × *Catostomus*	5.0	52	......	1	1	7	12	16	5	......	......	42	51
Catostomus × *Pantosteus*	1.4	15	6	1	26	2	5	4	3	15	17	79	87
Scales around caudal peduncle													
Catostomus × *Catostomus*	10.6	36	......	......	......	1	24	19	2	......	......	46	59
Catostomus × *Pantosteus*	3.6	15	3	4	12	6	26	14	11	8	......	84	49
Caudal peduncle, depth													
Catostomus × *Catostomus*	3.2	4	3	2	4	7	3	5	4	2	22	52	121
Catostomus × *Pantosteus*	10.2	11	11	4	14	8	18	11	7	3	......	76	26
Head length													
Catostomus × *Catostomus*	16.9	6	6	5	3	8	12	10	10	9	4	67	58
Catostomus × *Pantosteus*	17.2	6	3	......	4	10	12	7	3	3	5	47	63
Head depth													
Catostomus × *Catostomus*	12.3	8	7	4	5	9	19	11	10	5	4	74	50
Catostomus × *Pantosteus*	12.7	8	......	......	1	17	13	6	4	......	......	41	48
Head width													
Catostomus × *Catostomus*	3.6	2	1	2	2	2	......	3	......	1	2	13	47
Catostomus × *Pantosteus*	10.8	7	1	5	5	6	9	21	11	6	5	69	69
Isthmus width													
Catostomus × *Pantosteus*‡	36.7	61	......	......	2	29	33	13	3	......	......	80	45
Snout length													
Catostomus × *Catostomus*	5.4	5	3	1	1	4	6	4	4	2	3	28	57
Catostomus × *Pantosteus*	12.4	11	5	5	4	12	8	19	2	2	11	68	67
Mouth width													
Catostomus × *Catostomus*	7.8	10	14	2	10	4	8	11	2	6	13	70	49
Catostomus × *Pantosteus*	36.2	44	......	2	7	29	24	15	2	1	......	80	43
Cartilaginous ridge, width													
Catostomus × *Catostomus*	7.5	21	3	2	1	14	20	13	8	7	7	75	63
Catostomus × *Pantosteus*	22.9	56	......	......	1	26	44	8	1	......	......	80	44
Mouth length													
Catostomus × *Catostomus*	3.3	6	14	1	9	1	2	9	6	8	8	58	48
Catostomus × *Pantosteus*	24.7	42	3	1	......	18	28	13	12	1	3	79	57
Lower lip, union													
Catostomus × *Catostomus*	3.6	30	13	13	4	13	7	13	5	5	3	76	26
Catostomus × *Pantosteus*	22.1	141	......	......	4	31	37	7	1	......	......	80	30
Dorsal fin to occiput, distance§													
Catostomus × *Catostomus*	19.6	8	4	5	6	6	20	13	7	6	4	71	52
Dorsal fin base§													
Catostomus × *Catostomus*	32.0	14	1	4	6	10	20	23	11	1	......	76	52
Depressed dorsal fin, length§													
Catostomus × *Catostomus*	29.3	10	4	2	6	14	21	22	3	1	1	74	44
All counts													
Catostomus × *Catostomus*	......	39	......	1	7	44	127	60	41	......	1	281	55
Catostomus × *Pantosteus*	......	14	50	36	53	46	80	52	62	29	33	441	47
All measurements													
Catostomus × *Catostomus*	......	10	73	43	57	92	138	137	70	53	71	734	54
Catostomus × *Pantosteus*	......	39	23	17	42	186	226	120	46	16	24	700	48
All counts and measurements	......	2–30	143	93	144	194	314	253	189	96	126	1552	53
	......	36–141	3	4	15	174	257	116	30	2	3	604	47
Grand summary	......	23	146	97	159	368	571	369	219	98	129	2156	51

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* The averages in these two columns are weighted by number of specimens, and differences of less than 4 per cent are considered in these computations. The amount of difference refers to the actual counts, or to measurements expressed in thousandths of the standard length.

† Weighted averages, based on the original, unclassed data.

‡ This measurement differs little, and was not taken for the interspecific hybrids, within the genus *Catostomus*.

§ These measurements were taken only for the *Catostomus* × *Catostomus* hybrids.

TABLE XXXIX

Frequencies of Average Hybrid Index for Each Individual of Each Combination

An average index of 50 indicates exact intermediacy, on a scale in which the average value for the more primitive parental species is set at 0, and that for the more specialized parental species at 100. Indices are disregarded when the difference between the parental species is less than 4 per cent.

Hybrid Combination	Average Hybrid Index for Each Individual											No.	Ave.*
	−4.9 to 5.0	5.1 to 15.0	15.1 to 25.0	25.1 to 35.0	35.1 to 45.0	45.1 to 55.0	55.1 to 65.0	65.1 to 75.0	75.1 to 85.0	85.1 to 95.0	95.1 to 105.0		
Catostomus commersonnii sucklii × *Catostomus catostomus griseus*	.....	1	.....	1	.....	.....	2	.....	1	.....	.....	5	49
Catostomus macrocheilus × *Catostomus syncheilus syncheilus*	4	3	6	5	4	13	6	14	6	3	4	68	53
Catostomus macrocheilus × *Catostomus syncheilus palouseanus*	.....	.....	.....	.....	.....	1	2	.....	.....	.....	.....	3	56
Catostomus commersonnii sucklii × *Pantosteus jordani*	.....	.....	.....	.....	1	1	.....	.....	.....	.....	.....	2	43
Catostomus commersonnii sucklii × *Pantosteus delphinus delphinus*	.....	.....	.....	2	1	1	1	.....	2	.....	.....	7	53
Catostomus insignis × *Pantosteus clarkii*	.....	.....	.....	3	6	7	4	1	.....	.....	.....	21	48
Catostomus, species × *Pantosteus santa-anae*	1	3	5	5	6	9	5	2	1	1	.....	38	41
Catostomus tahoensis × *Pantosteus lahontan*	.....	1	2	2	1	1	1	.....	1	1	.....	10	44
Catostomus catostomus griseus × *Pantosteus jordani*	.....	.....	.....	.....	.....	1	.....	.....	.....	.....	.....	1	45
Catostomus latipinnis discobolus × *Pantosteus delphinus utahensis*	.....	.....	.....	.....	1	.....	.....	.....	.....	.....	.....	1	43
Totals													
Catostomus × *Catostomus*	4	4	6	6	4	14	10	14	7	3	4	76	53
Catostomus × *Pantosteus*	1	4	7	12	16	20	11	3	4	2	.....	80	45
Grand totals	5	8	13	18	20	34	21	17	11	5	4	156	49

* Based on original, unclassed data.

ter indices of mouth and lip structures average 42 (Table XII). The averages of the summary hybrid indices for all the characters in each individual vary from 41 to 56 for each of the 10 combinations, with a grand average of 49—again very close to exact intermediacy (Table XXXIX; Fig. 8).

For a few characters the hybrid indices tend toward a trimodal distribution, with modes below 0 and near or above 100 as well as the submeridian one (Table XXXVIII). This is true of the indices for dorsal ray counts, despite the fact that the average number of rays of this fin in the hybrids lies between the means for the parental species (Table XXXII). The reason is that the averages for the parental species of certain crosses differ by less than 1.0 ray so that the counts for the hybrid, necessarily whole numbers, often fall beyond the mean for either parental species. The hybrid counts must all fall beyond either the one or the other of the parental means in the combination, *Catostomus tahoensis* × *Pantosteus lahontan,* for in this cross the means for the parental species, respectively 10.38 and 10.10, both lie between two integers; if the hybrid count is 10 the index will be above 100, if 11, below 0. A tendency toward extreme indices is also shown for the counts of scales above and below the lateral line and for the depth of the caudal peduncle, because the *Catostomus,* species × *Pantosteus santa-anae* hybrids tend to have high values for these characters (see p. 49). The hybrid indices cluster close about the mean value of 50, for the characters by which the parental species on the average differ by more than 30 per cent (Table XXXVIII, next to last row).

The tendency toward intermediacy pervades the whole structural system of the organism, involving internal as well as external characters. In this respect, too, the sucker hybrids agree with interspecific crosses in other fish families—for instance in the Pleuronectidae (Hubbs and Kuronuma, 1942). The intercalation of the catostomid hybrids between the parental species in structural features is particularly well shown by the mouth characters (as demonstrated through the preceding text, in Tables XI–XII, in Figs. 3–4; and as illustrated in Pls. I, II, and IV). Differences in color of peritoneum, length of intestine, and size of air bladder are also involved. As shown by Figure 6 and Table XXIII the degree of development of the parietal fontanelle is intermediate in the hybrid between *Catostomus,* species and *Pantosteus santa-anae* (the 2 larger *C. commersonnii* × *P. delphinus* hybrids fail to show such intermediacy, and the *C. insignis* × *P. clarkii* cross was not studied in this regard). No other explanation than that of hybridization would seem capable of explaining the interposition of the whole array of characters between those of 2 species.

An intermediate type of relative growth in 1 hybrid is indicated by plotting the character index based on the lip and isthmus structures (Fig. 4).

In all ways, therefore, the hybrids tend to be intermediate between the species which miscegenated to produce them, and the intermediacy is often highly specific; that is, the hybrids have characters which lie between those

TABLE XL

FREQUENCIES OF COEFFICIENTS OF VARIABILITY (V) IN CATOSTOMID HYBRIDS AND IN THE PARENTAL SPECIES

	Coefficients of Variability								No.	Ave.*
	2.0 to 3.9	4.0 to 5.9	6.0 to 7.9	8.0 to 9.9	10.0 to 11.9	12.0 to 13.9	14.0 to 15.9	16.0 to 17.9		
Ray counts (Tables VIII, XXVI, XXXII)										
Parental species 1†	4	9	......	......	......	......	......	......	13	4.5
Hybrids	2	8	......	......	......	......	......	......	10	4.6
Parental species 2‡	3	10	......	......	......	......	......	......	13	4.5
Scale counts (Tables XXXIII–XXXVII)										
Parental species 1	2	12	22	7	2	......	......	......	45	6.7
Hybrids	1	9	8	4	2	......	3	4	31	8.8
Parental species 2	......	11	15	13	4	1	......	1	45	7.8
Character index, scale and ray counts (Table V)										
Parental species 1	......	1	1	......	......	......	......	......	2	6.1
Hybrids	......	1	......	......	......	......	......	......	1	4.6
Parental species 2	......	2	......	......	......	......	......	......	2	4.8
Character index, scale counts (Table XVIII)										
Parental species 1	......	......	......	1	......	......	......	......	1	8.0
Hybrids	......	1	......	......	......	......	......	......	1	5.1
Parental species 2	......	1	......	......	......	......	......	......	1	5.7
Character index, proportions (Tables VII and XI)										
Parental species 1	2	4	3	......	......	......	......	......	9	5.4
Hybrids	......	2	1	3	......	......	......	......	6	6.9
Parental species 2	1	2	3	......	2	......	1	......	9	8.0
Totals, for counts and indices										
Parental species 1	8	26	26	8	2	......	......	......	70	6.1
Hybrids	3	21	9	7	2	......	3	4	49	7.5
Parental species 2	4	26	18	13	6	1	1	1	70	7.1

* Based on original, unclassed data.

† The coarse-scaled *Catostomus* in the *Catostomus* × *Catostomus* crosses and the *Catostomus* species in the *Catostomus* × *Pantosteus* hybrids.

‡ The fine-scaled *Catostomus* in the *Catostomus* × *Catostomus* hybrids and the *Pantosteus* species in the *Catostomus* × *Pantosteus* crosses.

of the particular forms with which they are associated. This particularized intermediacy may be seen in external features of general appearance (as shown on Pls. III to VII); particularly well in mouth structures (p. 34; Pls. I–II); also in size of scales, including the squamational pattern (pp. 22, 30, 37, 40, and 43; Pl. V; Fig. 7), and in many other characters. By such relations the interpretation of the variant suckers as hybrids is strongly verified.

As evidence of hybridity, a point of outstanding importance is that several uncorrelated characters in the same set of specimens show intermediacy between the same pair of species. Thus, the suckers of the Columbia River system which are intermediate between *C. macrocheilus* and *C. syncheilus* in the number of scales and dorsal fin rays (Fig. 1) also show intervening values in the relative length of the depressed dorsal fin and of the distance forward to the occiput (Fig. 2). The uniform tendency toward intermediacy is witnessed by almost the entire body of data in the present study.

All of the data on the interspecific hybrids in the Catostomidae therefore conform to the rule that simple Mendelian segregation is seldom displayed in the inheritance of the systematic characters of fishes (Hubbs, 1940: 205–9). This rule holds whether the differences between the parental species be qualitative or quantitative and whether the differences be large and striking, or so minor as to be demonstrable only by statistical analysis. Uniformly, the offspring exhibit intermediate characteristics. They do not grade from the one extreme of one parental species to the opposite extreme of the other form involved in the cross: for any character the frequency distribution is in general similar to that displayed by each parental species (Figs. 1–3, 5, 7; Tables V, VII, VIII, XI, XVIII, XXVI, XXXII–XXXVII). The tendency for the hybrid indices to cluster about the point (50) of exact intermediacy (Tables XII, XXXVIII–XXXIX; Fig. 8) confirms the same principle. There is, of course, a theoretical possibility that Mendelian segregation may obtain, for there is a conceivable (though remote) chance that all characters show a balance between dominance and recessiveness.

For each character and for all characters combined, the hybrids seem to show little if any increase in variability as compared with the parental species. This conclusion, based on an inspection of the figures and tables, has been confirmed by computing and summarizing the coefficients of variability (V). The coefficients have the same order of range and of magnitude in the hybrids that they do in the parental species (Table XL). The slightly higher average coefficients shown by the hybrids for certain features is to be explained as a consequence of the smaller samples, which cause the values of V to fluctuate; a few values are sufficiently high to raise the average a little.

The fact that the coefficients of variability are not notably increased in the hybrids conforms to the principle that systematic characters show a seemingly Galtonian type of inheritance. Obviously there has been no large amount of error in the identification of the hybrids, for if there had been many mistakes, the variability would have been greater. Clearly, too, there can have been little backcrossing between the hybrids and the parental species, for this would also have led to a marked increase in variability.

Since, so far as we have discovered, there has been little if any backcrossing between the catostomid hybrids and their parental species and no real hybrid populations have been built up, we are unable to indicate that interspecific hybridization has played a role of any speciational importance in the Catostomidae. The fact that *Catostomus syncheilus* is intermediate in many respects between *Catostomus macrocheilus* and *Pantosteus jordani*—two other species of the Columbia River system—suggests the possibility that it may have arisen through the hybridization of those forms. *C. syncheilus,* however, shows its full specific distinctness in certain peculiar features, by its occurrence in many places with only one or with neither of the other species, and by the fact that it breaks up into its own series of local races. The approach toward *Pantosteus* also displayed by *Catostomus catostomus* conceivably could have been due to past hybridization, followed by backcrossing and inbreeding. It is our opinion, however, that the characters which *Catostomus syncheilus* and *C. catostomus* share with *Pantosteus* are the products of parallel evolution, for all of these features can be related to life on the bottom of swift, shallow streams. Such parallelisms are abundantly illustrated by fresh-water fishes (Hubbs, 1940, 1941*b*).

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PLATE I

Mouths of sucker hybrids and parental species

Drawn by Grace Eager

The enlargements were adjusted so that the specimens of the parental species (*a* and *c*) were represented as if they were of the same size as the hybrid (*b*).

FIG. 1*a*. *Catostomus*, species: U.M.M.Z. No. 131665, 153 mm. in standard length, from Sespe Creek, Ventura County, California.

FIG. 1*b*. Hybrid: U.M.M.Z. No. 131666, 114 mm. long, from the same collection.

FIG. 1*c*. *Pantosteus santa-anae:* U.M.M.Z. No. 131657, 95 mm. long, from pond off Piru Creek, Ventura County, California.

FIG. 2*a*. *Catostomus tahoensis:* U.M.M.Z. No. 124855, 83 mm. long, from Carson River, Churchill County, Nevada.

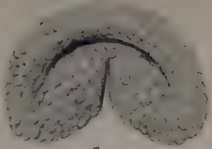
FIG. 2*b*. Hybrid: U.M.M.Z. No. 124861, 84 mm. long, from the same collection.

FIG. 2*c*. *Pantosteus lahontan:* U.M.M.Z. No. 124856, 84 mm. long, from the same collection.

FIG. 3*a*. *Catostomus insignis:* U.M.M.Z. No. 121641, 91.5 mm. long, from Middle Fork of East Branch of Black River, Apache National Forest, Arizona.

FIG. 3*b*. Hybrid: U.M.M.Z. No. 121642, 94 mm. long, from the same collection.

FIG. 3*c*. *Pantosteus clarkii:* U.M.M.Z. No. 121640, 90.5 mm. long, from the same collection.



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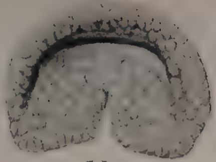

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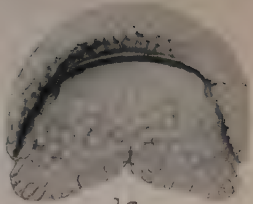

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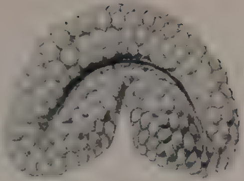

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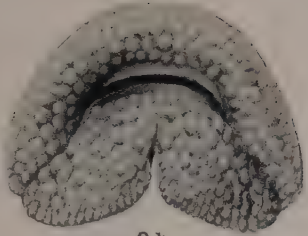

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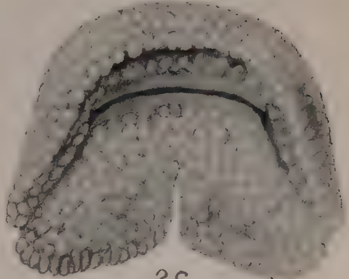

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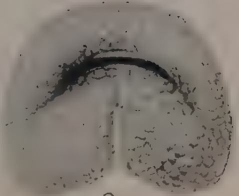

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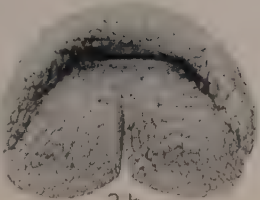

3b

G. Eager

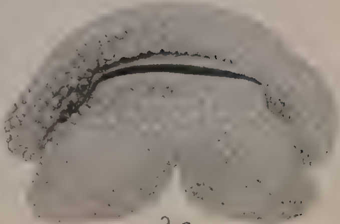

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PLATE III

Hybrid sucker, *Catostomus commersonnii sucklii* × *Catostomus catostomus griseus,* and the parental species

Photographed by Clarence Flaten

FIG. 1. *Catostomus commersonnii sucklii:* U.M.M.Z. No. 132229, 155 mm. in standard length, from Laramie River, Albany County, Wyoming.

FIG. 2. Hybrid: U.M.M.Z. No. 132230, 152 mm. long, from the same collection.

FIG. 3. *Catostomus catostomus griseus:* U.M.M.Z. No. 132217, 156 mm. long, from North Platte River, east of Parco, Carbon County, Wyoming.

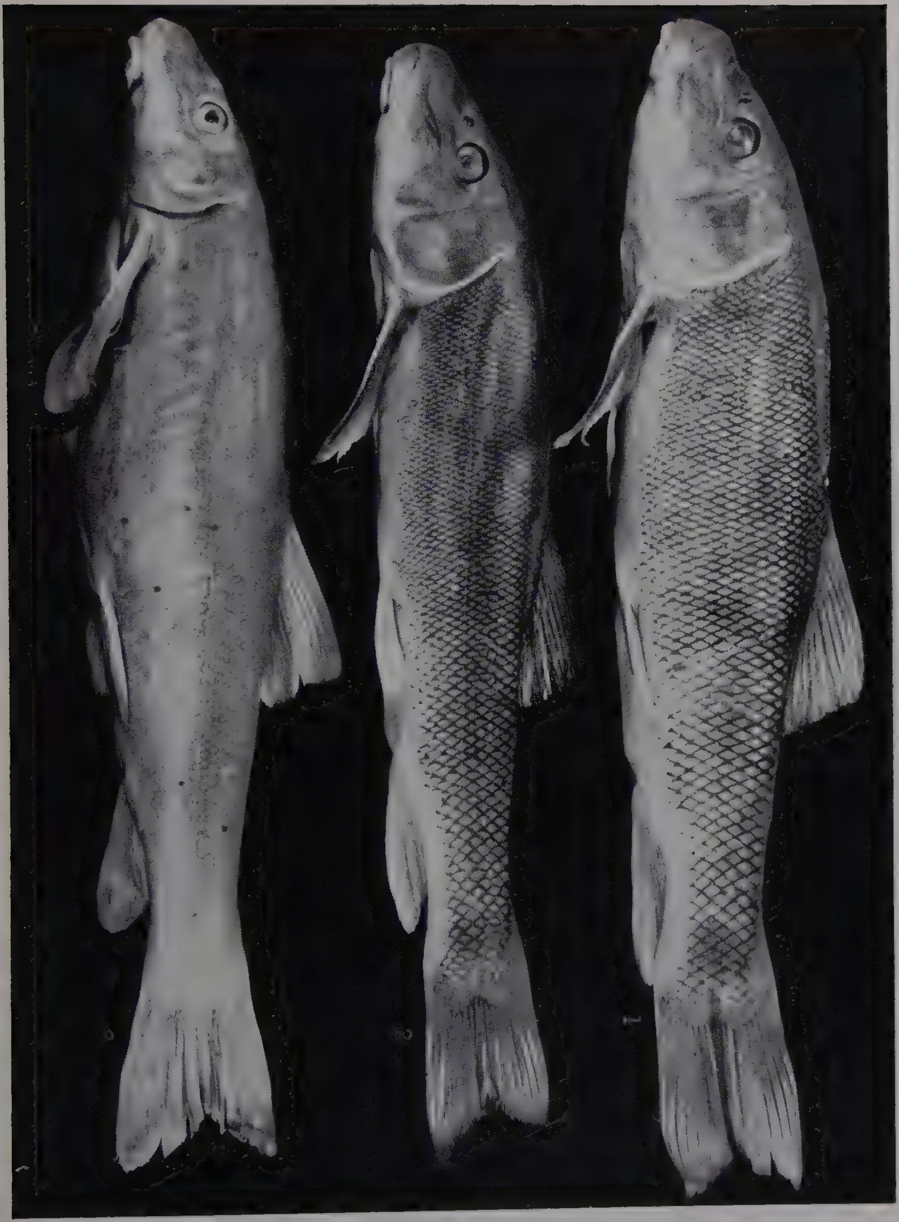


PLATE IV

Hybrid sucker, *Catostomus commersonnii sucklii* × *Pantosteus jordani,* and the parental species

Photographed by Clarence Flaten

FIG. 1. *Catostomus commersonnii sucklii:* U.M.M.Z. No. 132236, 55 mm. in standard length, from Lodgepole Creek, Kimball County, Nebraska.

FIG. 2. Hybrid: U.M.M.Z. No. 120375, 56 mm. long, from Grace Coolidge Creek, Custer County, South Dakota.

FIG. 3. *Pantosteus jordani:* U.M.M.Z. No. 120378, 55 mm. long, from Stockade Beaver Creek, Weston County, Wyoming.

PLATE IV

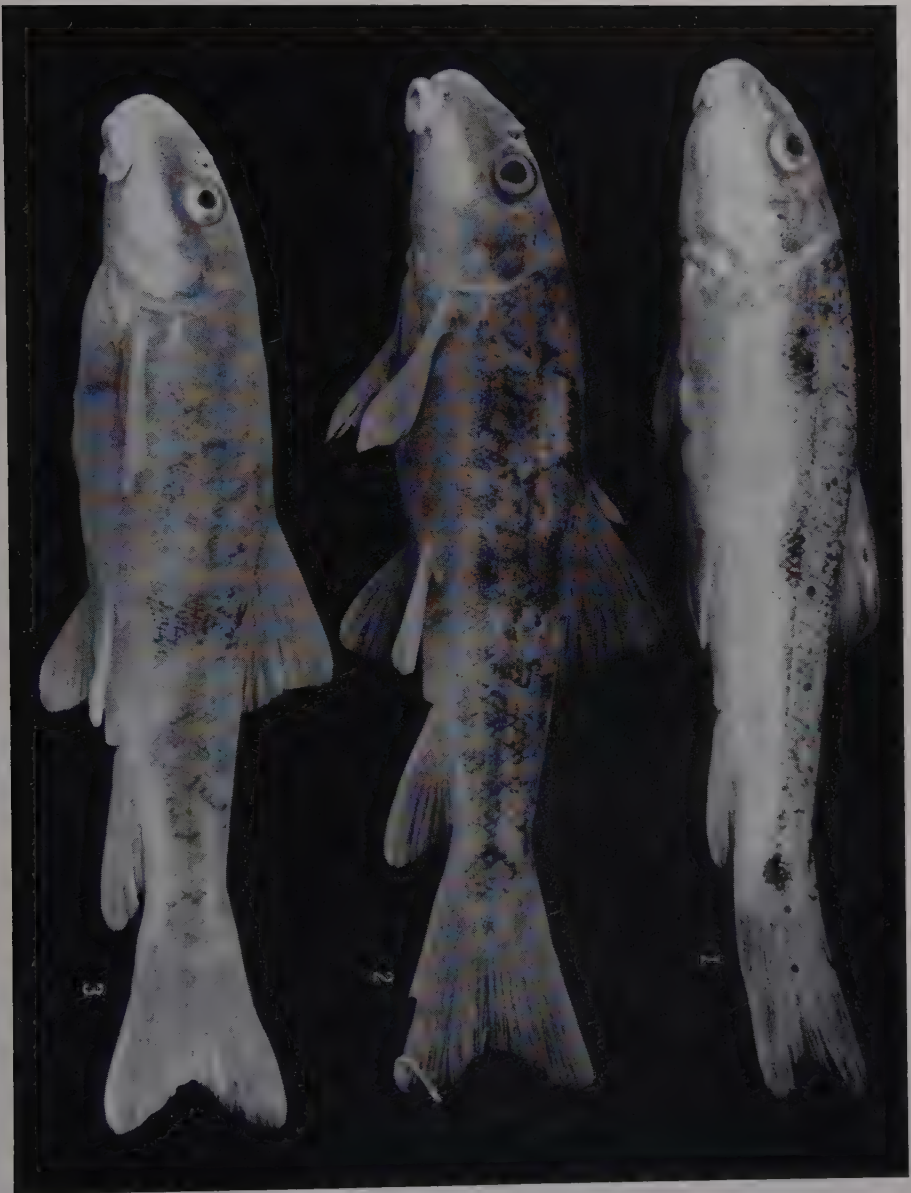


PLATE V

Hybrid sucker, *Catostomus commersonnii sucklii* × *Pantosteus delphinus delphinus,* and the parental species

Photographed by Clarence Flaten

FIG. 1. *Catostomus commersonnii sucklii:* U.M.M.Z. No. 132218, 127 mm. in standard length, from the North Platte River, Carbon County, Wyoming.

FIG. 2. Hybrid: U.M.M.Z. No. 136912, 128 mm. long, from Dry Creek, 3 miles west of Olathe, Montrose County, Colorado.

FIG. 3. *Pantosteus delphinus delphinus:* U.M.M.Z. No. 113424, 123 mm. long, from Green River, at Green River, Wyoming.

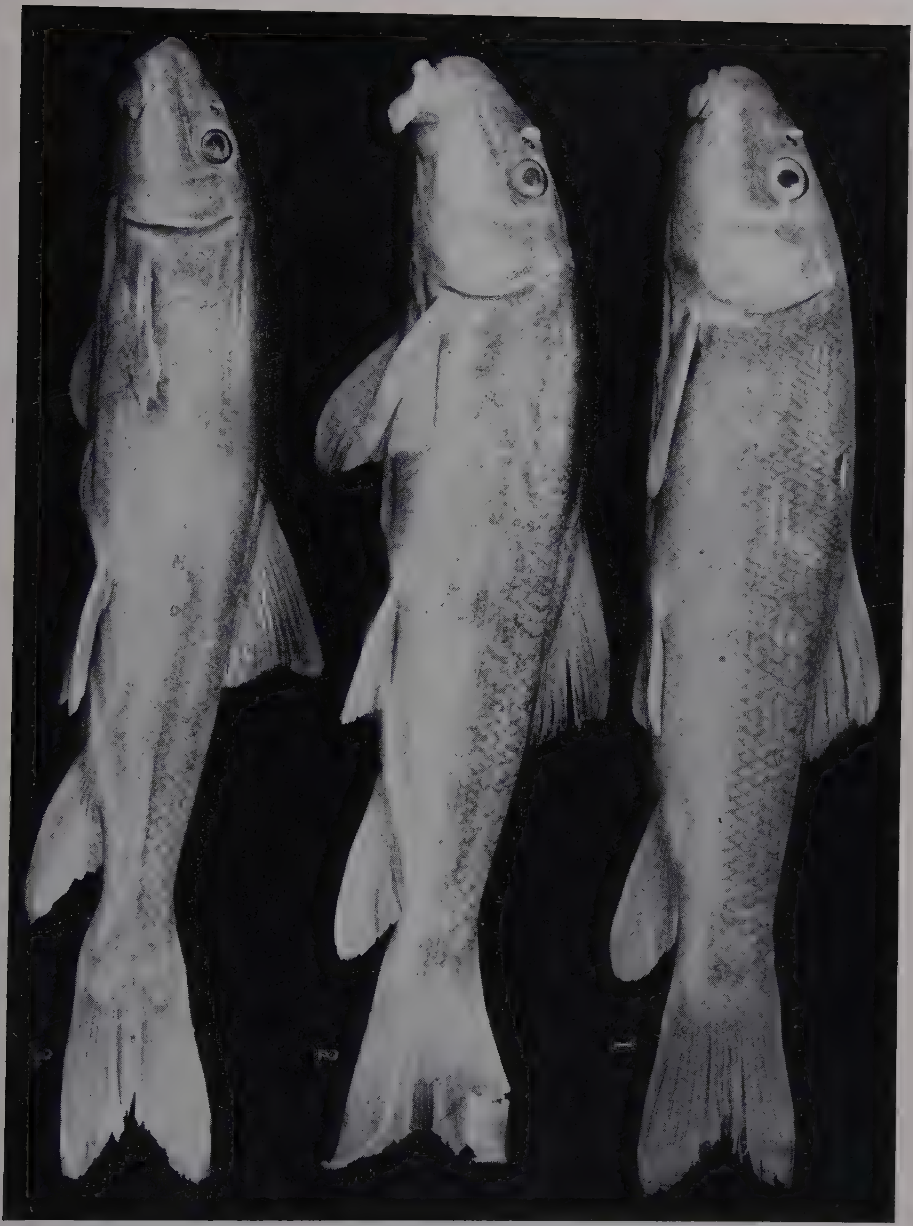


PLATE VI

Heads of sucker hybrids and their parental species

Photographed by Clarence Flaten

FIG. 1*a*. *Catostomus macrocheilus:* U.M.M.Z. No. 130470, 149 mm. in standard length, from Sucker Creek above Rockville, Malheur County, Oregon.

FIG. 1*b*. Hybrid: U.M.M.Z. No. 130471, 150 mm. long, from the same collection.

FIG. 1*c*. *Catostomus syncheilus syncheilus:* U.M.M.Z. No. 130469, 138 mm. long, from the same collection.

FIG. 2*a*. *Catostomus macrocheilus:* U.M.M.Z. No. 98721, 202 mm. long, from Smokle Creek, north of Almota, Whitman County, Washington.

FIG. 2*b*. Hybrid: U.M.M.Z. No. 98709, 204 mm. long, from South Fork of the Palouse River, Whitman County, Washington.

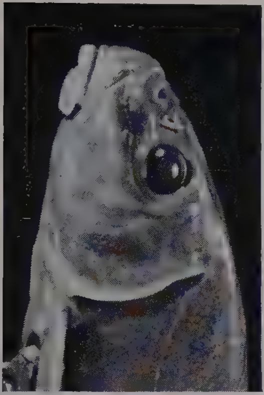
FIG. 2*c*. *Catostomus syncheilus palouseanus:* U.M.M.Z. No. 98707, 178 mm. long, from the same collection.

FIG. 3*a*. *Catostomus insignis:* U.M.M.Z. No. 110431, 105 mm. long, from Taylor Creek, Gila National Forest, New Mexico.

FIG. 3*b*. Hybrid: U.M.M.Z. No. 110433, 110 mm. long, from the same collection.

FIG. 3*c*. *Pantosteus clarkii:* U.M.M.Z. No. 124743, 111 mm. long, from Gila River at Cliff, Grant County, New Mexico.

3a



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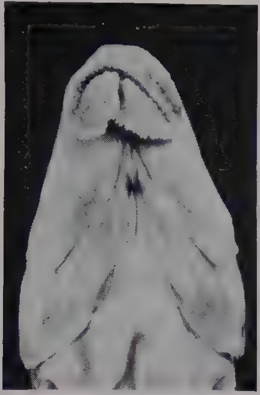

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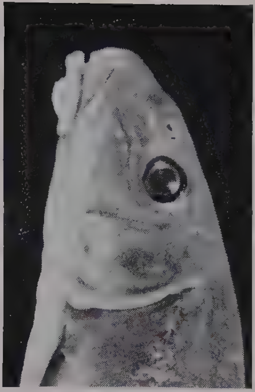

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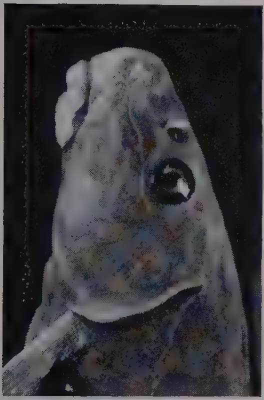

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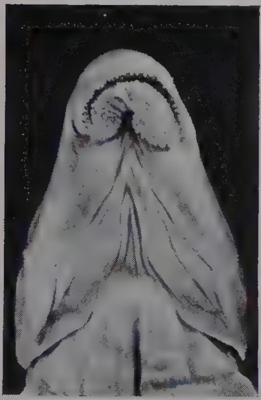

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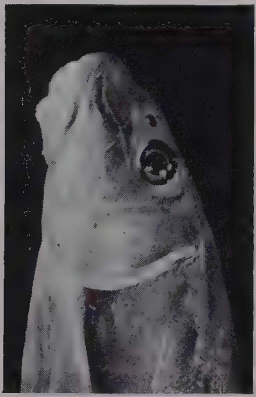

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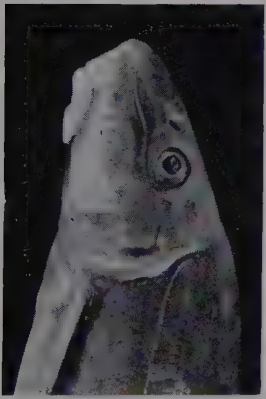

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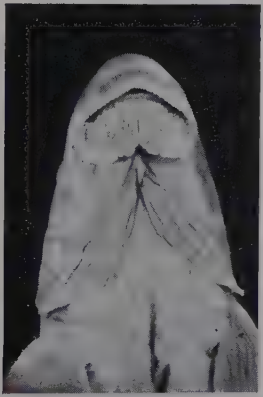

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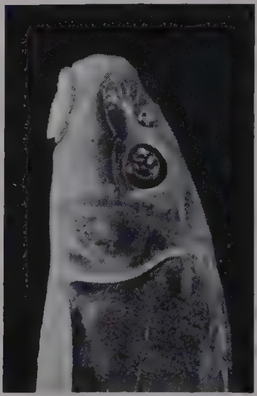


PLATE VII

Heads of sucker hybrids and their parental species

Photographed by Clarence Flaten

FIG. 1*a*. *Catostomus*, species: U.M.M.Z. No. 133857, 119 mm. in standard length, from Santa Clara River, Ventura County, California.

FIG. 1*b*. Hybrid: U.M.M.Z. No. 131666, 114 mm. long, from Sespe Creek, Ventura County, California.

FIG. 1*c*. *Pantosteus santa-anae:* U.M.M.Z. No. 131756, 115 mm. long, from North Branch of Warm Spring Creek, San Bernardino County, California.

FIG. 2*a*. *Catostomus tahoensis:* U.M.M.Z. No. 124912, 114 mm. long, from Humboldt River, Elko County, Nevada.

FIG. 2*b*. Hybrid: U.M.M.Z. No. 133688, 122 mm. long, from Little Truckee River, Nevada County, California.

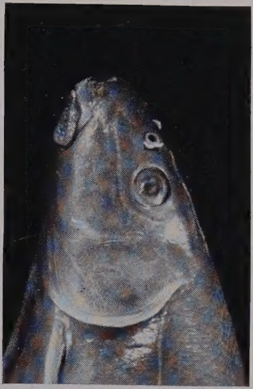
FIG. 2*c*. *Pantosteus lahontan:* U.M.M.Z. No. 124869, 119 mm. long, from Humboldt River at Irish-American Dam, Pershing County, Nevada.

FIG. 3*a*. *Catostomus catostomus griseus:* U.M.M.Z. No. 132217, 95 mm. long, from North Platte River, Carbon County, Wyoming.

FIG. 3*b*. Hybrid: U.M.M.Z. No. 127541, 98 mm. long, from Sweetwater River, Fremont County, Wyoming.

FIG. 3*c*. *Pantosteus jordani:* U.M.M.Z. No. 127540, 99 mm. long, from the same collection.

Plate VII



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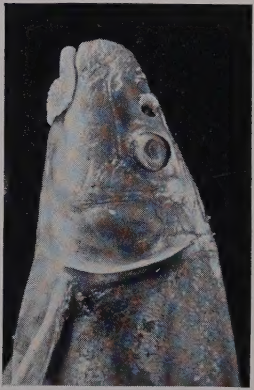

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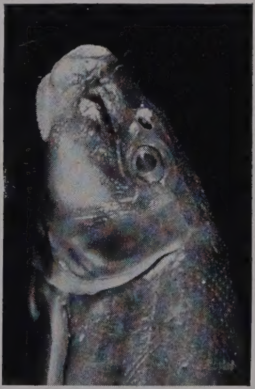

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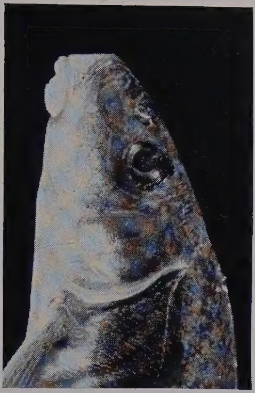

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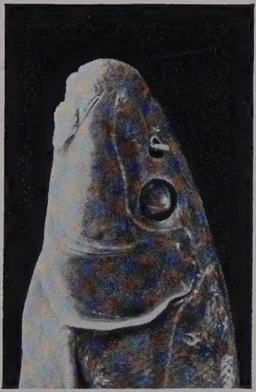

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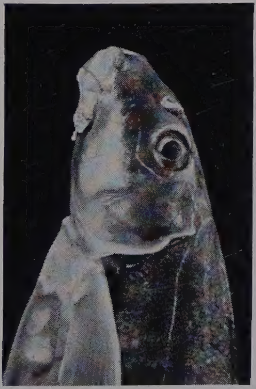

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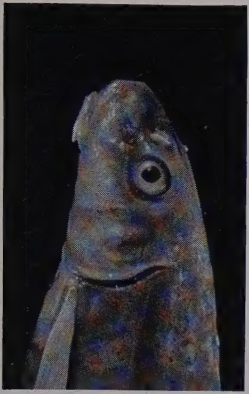

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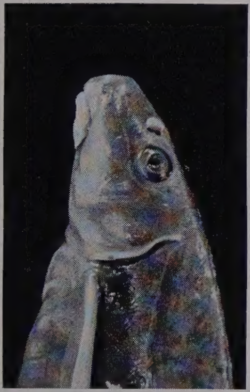

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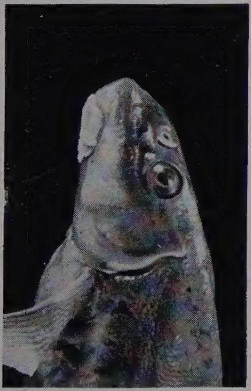

3c